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SOME NORTH AMERICAN FISH TREMATODES

WITH 6 PLATES, 2 CHARTS AND 1 TEXTFIGURE

BY

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under the direction of Henry B. Ward
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THESIS

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INTRODUCTION

The study of the parasites of North American fish, especially marine species, offers a comparatively new field to the investigator. Linton has opened this field in a broad sense by his papers on fish parasites of the Woods Hole region and of the Atlantic waters of Southern United States. This pioneer work has been necessarily incomplete in some respects. On the parasites of fishes inhabiting the colder waters of the northern Atlantic, almost no work has been done in America. Stafford and Cooper have made small collections in these regions. On European shores considerably more research has been done, and here the early work of Van Beneden, Olsson, and Levinsen has been followed by valuable contributions from Looss, Odhner, Lebour, Nicoll, and others.

The present paper is based very largely upon studies of marine fish parasites from the Maine coast. These studies were first undertaken at the Mount Desert Island Biological Laboratory during the summer of 1924, although some material was also collected in the same region in 1923. Early in the work of collection, attention was directed to a common trematode (*Otodistomum cestoides*) of the barn-door skate. Considerable time was devoted to the structure of this form and its life history. Later, a large series of fresh-water forms related to this species were also studied and compared. A brief report of the trematodes collected from marine fish has already been published (Manter, 1925).

Sincere appreciation is here extended to Professor Ulric Dahlgren for the use of the laboratory facilities at the Mount Desert Island Biological Station. Acknowledgment is also rendered to the Hygienic Laboratory of the U. S. Public Health Service and to the U. S. National Museum for the loan of valuable material. Above all, is the writer indebted to Dr. Henry B. Ward, under whose direction these studies were undertaken. To him appreciation is extended, not only for his constant interest, but also for the loan of material from his personal collection of parasites, and for the use of his extensive library. To others, who, like fellow-students, have been less intimately associated with this work, but who have gladly cooperated in many ways, gratitude is likewise expressed.

MATERIAL AND METHODS

The collection of parasites was not limited to any particular group. In general, a broad collection of metazoan fish parasites was attempted. The final collection included trematodes, cestodes, nematodes, acantho-

cephala, copepods, leeches, an ectoparasitic turbellarian, and an ectoparasitic isopod. From this collection the trematodes were chosen for special study.

The most common shore fish such as sculpin, flounder, herring, and skates were obtained from Frenchman's Bay in the immediate vicinity of the Laboratory. Most of the fish examined, however, were obtained at the small fishing village of Manset on the south side of Mount Desert Island. Here specimens of the larger food fish such as cod, haddock, and hake were available in large numbers. Identification of the host was usually simple as most of the fish examined were common and well known species. Some uncertainty was unavoidable in the correct identification of a few forms, such as the sculpins.

The following table (Table 1) shows the general occurrence of the different groups of parasites according to hosts.

TABLE 1

GENERAL DISTRIBUTION OF ENTOZOA IN HOSTS EXAMINED

Name of Host		Number of Hosts				
Scientific	Common	Examined	With Trematodes	With Nematodes	With Cestodes	With Acanthocephala
Acanthias vulgaris	Common dog fish	12		2	12	
Raia erinacea	Bonnet skate	8	1	1	8	
Raia diaphanes	Big skate	2			2	1
Raia stabuliforis	Barn-door skate	20	18	7	20	
Raia scabrata (?)	Skate	1		1	1	
Anguilla chrysypa	Common eel	2				2
Clupea harengus	Herring	28	9	6		
Osmerus mordax	Smelt	5	3	2		
Scomber scombrus	Mackerel	5		5		
Fundulus heteroclitus	Killifish, minnow	25	9		6	23
Tautogolabrus adspersus	Cunner	4		3		1

TABLE 1 (continued)

Name of Host		Number of Hosts				
Scientific	Common	Examined	With Trematodes	With Nematodes	With Cestodes	With Acanthocephala
Myxocephalus octodecimspinosus	Sculpin	11	3	7	4	9
Pholis gunnellus	Butterfish	9	2			
Anarrhichas lupus	Wolf-fish	2	1	1		
Zoarces anguillaris	Eel pout	1				1
Pollachius virens	Pollack	4	2	3		2
Gadus callarias	Cod	10	8	9	2	10
Melanogrammus aeglifinus	Haddock	17	4	9	5	17
Urophycis tenuis	Hake	3	3	1	1	2
Urophycis chuss	Squirrel hake	6	5	6	1	4
Hippoglossus hippoglossus	Halibut	2	1	2		2
Pseudopleuronectes americanus	Flounder	19	3	3	2	15
Limanda ferruginea (?)	Sand dab	2		2	2	1
Total		198	72	70	66	90

The barn-door skate (*Raia stabuliforis*) was found to furnish the most varied and interesting parasites. Ecto-parasitic on this skate were found; *Micropharynx parasitica* (a tri-clad turbellarian), *Aega psora* (an isopod), and a large leech, *Oxyostoma typica*.* In the nasal cavity was found *Charopinus dalmanni* (Retz.) a large parasitic copepod. The stomach was usually heavily infected with the trematode, *Otodistomum cestoides*. Large numbers of cestodes occurred in the spiral valve. Although only a part

* For the identification I am indebted to Prof. J. Percy Moore who reports that the leeches "are representatives of *Oxyostoma typica* Malm or possibly a closely related species of the same genus."

of this cestode material was examined, two forms were identified as *Rhynchobothrius erinaceus* (van Ben.) and *Acanthobothrium coronatum* (Rud.).

One interesting case of Acanthocephalan infection was found in *Fundulus heteroclitus.* The livers of these minnows were almost invariably heavily infected with a juvenile form of Neoechinorhynchus. These parasites were sometimes free in the liver tissue but usually were coiled in a very thin-walled cyst. In one liver 25 or 26 such cysts could be counted. Only two of about 25 specimens failed to show the cysts macroscopically. In one case, this same form of juvenile Acanthocephalan was found in the intestine. This possible occurrence of the parasite in the intestine led to feeding experiments. A Fundulus was isolated and fed liver containing cysts from other minnows. As some of the material was disgorged, it could not be ascertained exactly how many cysts were ingested. The fish was fed again on the following day, and killed and examined on the third day. Three of the Acanthocephala were found in the intestine. This experiment was repeated by again feeding an isolated Fundulus the cysts on two days, and examining it on the third day. This second fish contained six of the Acanthocephala in its intestine. It is evident that the parasite can be transmitted from the liver to the intestine of the same species host. A possible explanation of the rare occurrence of this type of transfer in nature is found in the fact that the viscera of dead minnows in the aquaria are readily devoured by the other minnows. No evidence was found that the parasite ever reaches sexual maturity in this host.

The final host of the parasite was found to be the common eel, *Anguilla chrysypa.* The locality from which the minnows were caught harbored numerous eels. Two of these fish were caught and examined for parasites. The first contained large numbers (about 50) of a Neoechinorhynchus in the lower part of the intestine. The parasites were apparently identical with the young form taken from the minnow, differing only in being sexually mature. The second eel contained three minnows in the stomach. One of these minnows was practically digested. From the stomach content in this region one of the Acanthocephalan cysts was recovered. Furthermore, there was found free in the upper part of the intestine one of the juvenile Acanthocephalans without the cyst. Lower down in the intestine occurred large numbers of the adult parasite attached to the intestine wall. The species of Acanthocephala was kindly identified by Dr. H. J. Van Cleave as *Neoechinorhynchus cylindratus* (Van Cleave).

The demonstration seems to be quite complete that the eel (at least in this particular locality) acquires (at least in part) its infection through the minnow, *Fundulus heteroclitus.* Whether the minnow is a necessary link in the life-history of the parasite is very doubtful. Van Cleave (1920) in explaining juvenile forms of Acanthocephala encysted in various fish,

suggests that they may result from ingestion of the larva when it is too young to maintain itself in the intestine, the immature larva developing to an infective juvenile form in some tissue outside the digestive tract.

In the course of the present work, no new methods of technique were discovered. The finding of the larger parasites such as most cestodes, acanthocephala, and nematodes is simple. To collect the smaller forms such as many trematodes, the content of the digestive tract of the host must be minutely examined. Best results were obtained by diluting a small amount of material with considerable water in a large glass dish. A changing from light to dark of the background below the dish is often helpful. Careful scraping of the wall of the digestive tract is usually necessary to remove many of the smaller parasites.

Cestodes were killed in $HgCl_2$ solution. Agitation by shaking or the actual stretching by hand of cestodes is necessary to prevent excessive contraction. Trematodes were killed according to the Looss method (Looss 1901) by first shaking in water and then in a 50% solution of $HgCl_2$. A modified Gilson's solution (Petrunkevitch solution) was also found very satisfactory for trematodes. Nematodes were killed by placing in hot 70% alcohol or hot Petrunkevitch solution. Acanthocephala from the marine fish were first placed in fresh water which causes complete extension of the proboscis. When the Acanthocephala no longer respond to stimuli they are removed to the killing solution.

Some difficulty was experienced by some forms, especially trematodes, later becoming quite black, due apparently to a precipitation of metallic mercury. This condition might be due to insufficient or delayed treatment with iodized alcohol. A semisatisfactory method of reclaiming such specimens was found to consist of treating them with a weak solution of nitric acid. The acid removes the mercury but slightly stains the tissues.

In staining trematodes for total mounts, Ehrlich's or Delafield's hematoxylin or a mixture of the two was found to be very satisfactory. Alum cochineal also gave good results. Sections were stained with the ordinary reagents such as hematoxylin, iron hematoxylin, safranin, eosin, orange G, and Lyon's blue.

The present studies can be divided into three rather distinct parts as follows. First, an intensive study of *Otodistomum cestoides*, its first larval form, its growth changes within the final host, and its morphology. Some data was also obtained from an attempt to trace the life history of this form. Second, a comparative study of the entire family of the Azygiidae, and a revision of the American representatives of the genus Azygia. Third, a briefer account of each of the other forms of marine trematodes in the collection. This last account also includes data on several forms from the collection of Dr. H. B. Ward. These latter were collected from the Woods Hole region.

HISTORICAL SURVEY

Van Beneden (1858 and 1871) was one of the earliest workers to deal particularly with fish parasites and many of the more common species were first described by him. His collections were made along the coast of Belgium. Olsson in 1868 records 32 different trematode parasites from Scandinavian fish. Twenty-seven of these parasites were distomes, and eight were reported as new. Olsson's work covered a wide host range, the trematodes being collected from 42 different species of fish.

Levinsen published in 1881 results of his studies on trematodes of arctic fish. This work is the product of two years spent on the west coast of Greenland and constitutes the first comprehensive record of trematodes from strictly arctic marine fish. The number of host species examined was small (six), but the trematode fauna of a few fish such as the sculpin was thoroughly studied. Nine different species of trematodes were recorded from this host. Levinsen lists thirteen different sexually mature forms, most of which are distomes. Seven species are described as new.

Early work on the fish trematodes of the Mediterranean was done by Rudolphi, Monticelli, Stossich, and Looss. The detailed and accurate morphological observations of Looss have been of special service, and his (1899) conception of the genus among distomes has resulted in a complete systematic reorganization of that group.

Probably the most important paper on trematodes of arctic fish is Odhner's contribution (1905) to the Fauna Arctica, *Trematoden des arktischen Gebietes*. This critical monograph of the arctic trematode fauna is not limited to fish parasites but includes a few forms from avian and mammalian hosts. Odhner also restudied Levinsen's material. As the paper deals with considerable change in the "natural system" of trematodes, short descriptions are given of some forms outside the arctic regions. Twenty-two different trematodes, 19 of which are Digenea, are recorded from fish. Among these fish trematodes, four new genera and three new species are described. Several previously known species are redescribed, and some important systematic reorganizations are made. In a series of later short papers under the general title, *Zum naturlichen System der digenen Trematoden*, Odhner has made numerous subsequent additions to our knowledge of relationships among the trematodes, and his conclusions have been largely accepted by Nicoll (1915) and others.

The trematodes of the British marine fish are probably better known than those of any other particular region. This is largely due to the researches of Lebour, Johnstone, T. Scott, A. Scott, and Nicoll. According

to Nicoll, up to 1915 nearly 100 species of trematodes had been recorded from British marine fish. Nicoll's (1915) list of trematodes from marine fish contains 241 different species of trematodes belonging to 119 genera. Of these trematodes, 157 species and 73 genera are distomes.

In America the work of Linton at Woods Hole, Beaufort, N. C., and the Tortugas stands almost alone. The last named region is especially interesting in revealing a very rich and varied trematode fauna (Linton 1911) with forms differing considerably from most of the more northern forms. Stafford (1904) gives a list of 37 trematodes from 32 different Canadian marine fish. Cooper (1915) gives more complete data on a few forms from the same region.

A large amount of the literature is, of course, in the nature of special studies on individual or few forms. Examples of papers of this type are found in the works of Poirier (1885), Villot (1879), Pratt (1898), Darr (1902), Buttel-Reepen (1903), and Mühlschlag (1914).

THE MORPHOLOGY OF *OTODISTOMUM CESTOIDES*

OTODISTOMUM CESTOIDES (VAN BENEDEN 1871)

Otodistomum cestoides (van Ben.)
Syns.: *Distomum cestoides* van Ben. 1871
Otiodistomum veliporum of Stafford 1904
Otiodistomum veliporum of Lebour 1908
Otiodistomum veliporum of Lönnberg 1891
From stomach, *Raia stabuliforis* (=*R. laevis*)
Reported hosts: *Raia batis*
Raia laevis
Raia fullonica
Raia lintea
Raia clavata
Raia radiata
Raia macrorhyncha
Chlamydoselache anguinea

Dist. cestoides was first obtained by van Beneden (1871) from *Raia batis.* The genus Otodistomum was named by Stafford (1904) for a form he obtained from the stomach of *Raia stabuliforis* (=*R. laevis*). This form he called *Otodistomum veliporum,* identifying it as the *Dist. veliporum* of of Creplin. The close resemblance between the two species *cestoides* and *veliporum* has been a cause of general confusion, and, indeed, the two have been considered synonymous. Odhner (1911b) first showed that *O. cestoides* (van Ben.) had been incorrectly identified as *O. veliporum* by previous workers including Stafford, Lebour, and Lönnberg. In the course of the present studies both species were available for comparison. Specimens of *O. veliporum* were obtained from the collection of Dr. H. B. Ward* and were collected by him from *Raia binoculata* in Alaska in 1909. Further material of this same form was collected by a fellow-student from the same host at Friday Harbor, Washington, in 1924. Frequent reference will be made to this species in connection with the following discussion of the morphology of *O. cestoides.*

The host records of the two species are doubtless somewhat confused. According to the literature, *O. veliporum* appears to have a much wider host range among the Selachians, *O. cestoides* being almost entirely restricted to Raia species. In the region of Mount Desert Island *O. cestoides* occurs abundantly in *Raia stabuliforis,* but was never found in any other species of skate. Both Stafford and Cooper report it from Canadian waters.

* Collection of Dr. H. B. Ward, vial No. 48a from Excursion Inlet, Alaska, July 22, 1909.

Linton also records it from Woods Hole but there it seems to be a rare parasite.

The trematode was found in the lower part of the pyloric stomach of *Raia stabuliforis*. It is one of the most common fish trematodes in the region of Mount Desert Island as almost all the skates of this species we re-infected, sometimes heavily. Only two individuals among twenty examined in 1924 were uninfected, while all of the several examined in 1923 contained the trematode. The average degree of infection is about 21, although the number varies from only 2 or 3 to about 150. In a number of cases only young immature forms were found. It is also common, especially if the infection is light, to find only mature forms or at least no very young specimens. Several instances were found wherein all stages were present. Table 2 shows a record of the collection of this parasite.

The trematode is one of the largest known. Stafford records worms as long as 80 mm. when extended. There is a remarkable size variation. The longest specimen in the present collection measured about 65 mm., while several were found only 2 or 3 mm. in length. Sexual maturity is reached when the worm has a length of about 11 mm.

The body form is elongate and somewhat flattened dorso-ventrally especially in the posterior region. The anterior end tapers slightly in front of the ventral sucker and is bluntly pointed. Behind the ventral sucker the body tapers only very gradually and the posterior end is usually blunt. In some cases, however, when the worm is extended the posterior tip is sharply pointed. In this case, the body form is spindle-like.

The two suckers are close together near the anterior end. The ventral sucker is the larger and very powerful. When in use this ventral sucker may be protruded from the body very prominently. The worms cling tenaciously by means of the ventral sucker and may extend the anterior end of the body for some distance, feeling about in a leech-like manner. When removed from their host the worms cling to each other by means of their ventral suckers, and it is often difficult to separate individuals after they have become attached in this manner. There is a marked tendency for the worms to bend slightly inward, (i.e., ventrad), so that in profile they assume a curved or crescentic shape. This shape is especially marked when the trematodes are killed unless they are prevented by some mechanical means from so curling. The color of the worms is a translucent white when alive, becoming opaque white when killed. The region of the uterus just posterior to the ventral sucker is dark brown in color, due to the presence of many eggs which possess a light brown shell.

The oral sucker is smaller than the ventral sucker and the size ratio of the two does not show any progressive change with growth, averaging the same in very small individuals as it does in the largest. The anterior sucker averages slightly over .6 the size of the ventral one, or a proportion of

TABLE 2

INDIVIDUAL INFECTION OF *Raia stabuliforis* WITH *Otodistomum cestoides*

Date	Content of Stomach	Number of parasites	Condition
July 16	Empty	Several	Mostly mature
	Sculpin	"	
" 27	Empty	None	
August 5	Empty	Few	Immature
	"	"	"
	"	8–10	
	"	30–35	
	"	15–20	
	"	10–15	
" 8	Crab, shrimp	16–20	Mature
	Remains of flounder	16	Small, immature
" 12	3 herring, part of lobster	16–20	Mature
	Empty	17	Small
	"	4–5	
" 19	"	Many	All sizes, 10 or more mature
	8–10 small crabs, shrimp	None	
	Empty	12–15	Mostly mature
	"	160–170	Heaviest infection. 100 immature
	Remains of fish, Buccinum	Several	All sizes
" 28	Flounder	2	Mature

about 3 : 5. Odhner (1911b), however, gives a ratio of 3 : 4 for *O. cestoides* and 3 : 5 for *O. veliporum*. Miss Lebour's single specimen with a ratio of 1 : 2 must have been (as Odhner suggests) an abnormal condition. For the measurements of the suckers see Table 4.

The circular opening of the oral sucker may be directed anteriorly, but is usually ventral. The ventral sucker is very deep, extending nearly to the dorsal surface of the body when the worm is extended. The cavity of this sucker extends posteriorly as well as dorsally, a condition due to the

greater development of its muscles in the posterior region. While interesting because of the high degree of muscular development, the structure of the two suckers is like that already described for similar forms by Poirier (1885) and for *O. veliporum* by Mühlschlag (1914).

From the ventral anterior rim of the ventral sucker two muscle bands pass dorsally and can be traced nearly to the longitudinal body muscles of the dorsal wall. Crossing them obliquely a strong band of muscles can be seen to extend ventrally and anteriorly from the central dorsal border of the sucker to the longitudinal muscles of the ventral body wall. There are also muscle fibers extending laterally from this anterior ventral border of the sucker. Muscle bands at the posterior border of the sucker extend laterally on each side, and other bands extend dorsally to the dorsal body wall.

Short muscles are attached to the anterior margin of the oral sucker and course anteriorly and dorsally where they seem to join longitudinal body muscles of the dorsal side. Just posterior to these occur lateral oblique muscles running dorsally and laterally from each side of the sucker. They also are closely related with the dorsal longitudinal body muscles. Some of these fibers extend to the outer edge of the sucker. Finally, from the posterior edge of the sucker oblique muscle bands run dorsally and posteriorly and attach themselves to the pharynx.

The body wall consists of the cuticula, a layer of circular muscles, and a layer of longitudinal muscles (Fig. 12). The cuticula is a thick structureless layer surrounding the entire body. In a specimen about 25 mm. in length, this cuticula was about 17μ thick on the ventral surface of the neck region and about 28μ thick on the ventral surface of the posterior region. The thicknesses on the dorsal surfaces of the same regions were 34 and 37μ. Hence, the same relative thicknesses are found that Mühlschlag noted for *O. veliporum*. For the latter species, Mühlschlag's measurements are all much smaller than were found in the present species, but the size of the specimen was not given in the former case. The cuticula is much thinner over the inner surfaces of the two suckers. Here it measures only 5 to 8μ in thickness.

The body wall is thrown into circular folds which are more prominent with increased degree of contraction. These folds give the ringed appearance characteristic of this group of trematodes. Sections show that these folds involve the cuticula, and the layer of circular muscles, but not the layer of longitudinal muscles. The thickness of the circular layer, therefore, varies greatly. The layer is very thick in the center of the folds, and is greatly reduced in the furrows between the folds. In the following table a medium condition is represented as far as possible.

THICKNESS OF REGIONS OF BODY WALL
(Specimen about 25 mm. long)

	Neck Region	Testis Region	Posterior Region
	Ventral Surface		
Cuticula	17 μ	28–30μ	28–30μ
Circular muscles	40–50	50–55	50–55
Longitudinal muscles	34	17–20	17
	Dorsal Surface		
Cuticula	34 μ	40 μ	35–45μ
Circular muscles	50	50	38
Longitudinal muscles	22	20	16

The parenchyma presents no unusual features. It consists of a spongy tissue, filling in the regions between organs. Small nuclei are common, and also larger cells which are possibly nervous in function. The parenchyma is set through with muscle bands. Many of these, especially near the body wall, and within the neck region are oblique or diagonal, but the majority run in longitudinal bands throughout the length of the body. In species of Azygia (a related genus) a very definite and relatively narrow band of these longitudinal muscles occurs. In cross-section, the body is separated by them into medullary and cortical regions. Various Azygia species were available for comparison with *O. cestoides* in this respect. The localization of the muscles is much more pronounced and definite in Azygia where they form a rather compact layer. Here also the follicles of the vitellaria are outside this layer, that is, in the cortical region. In Otodistomum, the longitudinal parenchyma muscles are not limited to such a narrow layer and their formation is much less compact (Fig. 23). The region of their occurrence is, however, definite enough so that it can be noted that the follicles of the vitellaria lie largely internal to them, a condition to be contrasted with that occurring in Azygia species.

The nervous system could not be worked out in detail, only its more prominent features being noted. These agreed with data already known for similar forms.

The pharynx is ovoid or egg-shaped. It is located just posterior and slightly dorsal to the oral sucker. Its size is about 0.5 mm. by 0.3 to 0.4 mm. in average sized specimens. The largest examples measured about 0.75 mm. in length. In a specimen 24.5 mm. in length the pharynx measured 0.56 by 0.37 mm., and the thickness of its walls was about 0.18 mm. There is no pre-pharynx and the pharynx itself may protrude slightly into the cavity of the oral sucker. The pharynx usually extends obliquely dorsally and posteriorly. The opening between pharynx and oral sucker is therefore facing obliquely between a dorso-ventral and a posterio-anterior direction. The walls of the pharynx are very muscular and show the same sets of muscles found in the suckers. Circular or equatorial muscles are especially

powerful in the posterior region where the esophagus joins the pharynx and these may act as a sphincter muscle between the two (Fig. 10).

Special muscle bands run obliquely forward from the dorsal and ventral sides of the pharynx to the oral sucker. These bands are much more prominent on the ventral side. The degree of contraction of these muscles no doubt accounts for the varying position of the pharynx especially its tip in the dorso-ventral direction in relation to the oral sucker. Sometimes the pharynx entirely overlaps the sucker dorsally and rarely it extends almost directly posteriorly.

The pharynx leads directly into the esophagus. In a specimen about 25 mm. long the anterio-posterior length of the unpaired region of the esophagus adjacent to the pharynx is only about 57μ, but the organ divides immediately into two lateral stems and is actually a tube running laterally and perpendicular to the long axis of the pharynx. The length of each lateral stem is about 0.4 mm. Each stem bends toward the anterior and extends in that direction about 0.3 mm. before opening into the intestine proper (Fig. 10). The esophagus lies dorsal and partly lateral to the pharynx.

Outside the cuticula layer of the esophagus occurs a layer of circular muscles covered in turn by a thin coat of longitudinal muscles. The circular muscles are more prominent in the region where the esophagus joins the intestine, and serve here as a sphincter muscle usually giving rise to a slight constriction in this region. Usually at about the level of the middle of the pharynx the esophageal stems on each side open into the ceca of the intestine proper. The internal cuticular layer of the esophagus ends abruptly at this point (Fig. 10). The intestinal ceca continue forward for a short distance, then bend abruptly and lead posteriorly.

The intestine shows no special regions. The two branches stretch nearly to the posterior tip of the body. They spread apart in the region of the ventral sucker, but approach each other closely immediately posterior to the sucker. They are also forced somewhat laterally by the ovary and testes. Just behind the posterior testis they again approach each other slightly. As in other related trematodes (Azygia and Leuceruthrus), the ceca are thrown into small folds throughout their length, the folds being more pronounced the higher the degree of body contraction. Each branch of the intestine ends blindly. There may be a slight difference in their length. That no significance can be attached to the frequently unequal length of the ceca is shown by the fact that the right is sometimes longer and sometimes shorter than the left.

The intestine is lined internally by a layer of cuboid or low cylindrical cells from which long wavy protoplasmic processes stream out into the lumen usually nearly filling it (Fig. 10). The internal boundary of these intestinal cells is very indefinite. The size of the cells is the same in very

small specimens and in the largest. A thin membrane surrounds the intestine which is also provided with a thin circular (internal) and longitudinal (external) muscle layers.

The excretory system is like that of similar forms. It consists posteriorly of a large single median tube which may be much swollen, lying between the branches of the intestine, and opening by means of a short duct at the posterior tip of the body. This tube branches a short distance behind the posterior testis, its two branches crossing the intestinal ceca ventrally and proceeding anteriorly lateral to these ceca. The two branches are continuous anterior to the oral sucker.. The main excretory system consists then, of a Y-shaped tube with the two forks of the Y continuous. This tube may be thrown into folds comparable with those described for the intestine. Its outline in cross-section is very irregular and it can be seen to be continually receiving minute lateral branches. Its thin membraneous lining is obscured by many deeply staining spherical granules which thickly adhere to the wall of the main tube throughout its length. These concretions are generally considered as waste products, and are commonly known in many trematodes.

Flame cells are numerous. They are small cells oval in shape, with prominent nuclei. Favorable sections show that they occupy ends of minute excretory ducts and that their tips are prolonged into a tuft of cilia about equal to the cell body in length. The cells measure about 14 by 8μ.

The genital pore is ventral, median, between the two suckers and much closer to the oral sucker. It leads into a roomy genital atrium within which usually projects the nipple-shaped genital cone or papilla (Fig. 5). Both the genital atrium and the papilla are lined with cuticula which, however, becomes very thin at the tip of the cone. Just beneath this cuticula the wall of the atrium is strengthened by a thick layer of circular muscles. These muscles continue about the base of the papilla but gradually disappear toward its tip. Outside these circular muscles is a layer of longitudinal muscles, that is, muscles running in the direction of the long axis of the papilla. These muscles are continuous from the wall of the atrium into the papilla where they are internal to the circular muscles. Oblique muscles run off from the region of the longitudinal muscle layer of the atrium. In the solid-appearing tissue of the cone occur numerous nuclei which are more numerous near the tip of the papilla.

What at first appeared to be a marked difference in the size and occurrence of this papilla in the two species of Otodistomum led to a study of the permanency and variability of this organ. In the related genus Azygia, the genital atrium is usually without a papilla, the common sex duct opening at its base. This base of the atrium is, however, protrusible so that it can be thrust out papilla-like. Thus, here the genital papilla is only a momentary or temporary structure. Odhner (1911b: 518) says in

regard to this condition; "Dies konnte den Verdacht erwecken, dass es sich bei Otodistomum am Ende in derselben Weise verhielte; doch scheint mir dort die Papille einen mehr 'soliden' Eindruck zu machen."

Sections through *O. veliporum* from the Pacific showed the genital papilla almost always entirely absent or quite rudimentary in size. In *O. cestoides* the papilla was usually of robust form filling most of the atrium, or even entirely protruded from it (Fig. 6). In the latter case, the atrium itself is practically eliminated. In order to determine the constancy of the papilla, specimens of various sizes and degrees of body contraction were sectioned. Specimens collected in different years and killed in different solutions were also compared. The usual and contrasting conditions found are represented in Fig. 8 (*O. cestoides*) and Fig. 7 (*O. veliporum*). Of the specimens of *O. veliporum* sectioned, six showed the papilla absent, or a condition as in Azygia, three showed a small papilla (Fig. 7), while one showed a prominent papilla partially protruded from the pore (Fig. 29). Among eight specimens of *O. cestoides* sectioned, one showed the papilla entirely protruded (Fig. 6), six showed a robust papilla largely filling the genital atrium (Figs. 5 and 8), while one showed the papilla entirely absent (Fig. 28). Odhner's suspicion is therefore correct. Although the genital papilla has always been described and figured as a prominent feature in Otodistomum species it is capable of being entirely withdrawn as is normally the condition in Azygia. What appeared, then, to be a clear distinction between the two forms studied becomes a weak taxonomic character since it is variable and inconstant.

The atrium in *O. veliporum* from the Pacific almost constantly led very sharply posteriad and only slightly dorsad, while in the Atlantic form (*O. cestoides*) the slope of the atrium was almost directly dorsad and only slightly posteriad. This degree of slope of the atrium is probably associated with the condition of the papilla as when this structure was completely withdrawn in *O. cestoides* the atrium led sharply posteriad (Fig. 28).

Measurements on the size of the atrium and papilla in different specimens are as follows:

Otodistomum veliporum

	Genital atrium			Genital cone		
1.	0.845		0.093 mm.	0.102	by	0.08 mm.
2.	0.9	by	0.06	0.075		0.035
3.	0.935		0.112		absent	
4.	0.935		0.168	0.056		0.093
5.	0.935		0.149		absent	
6.	2.04		0.32		absent	
7.	1.57		0.3		absent	
8.	1.57		0.28		absent	
9.	1.25		0.23		absent	
10.	0.9		0.5	1.25		0.43

Otodistomum cestoides

	Genital atrium		Genital cone	
1.	0.243 ×	0.187 mm.	0.168 ×	0.149 mm.
2.	absent		0.71	0.52
3.	0.33	0.28	0.28	0.2
4.	0.617	0.355	0.317	0.317
5.	0.37	0.187	0.187	0.187
6.	0.6	0.6	0.39	0.54
7.	0.94	0.62	0.39	0.54
8.	1.25	0.15	absent	

It is certain that the size of the papilla is independent of general body contraction. Measurements No. 4 in the above table represent a strongly contracted specimen of *O. veliporum* and an extended specimen of *O. cestoides*. The size of this structure is also independent of the killing fluid. Sometimes the body wall projects lip-like about the genital pore. This condition also is not associated with the size of the papilla. A definite system of muscles about the papilla and in the neck region seems to be responsible for the protrusion and withdrawal of the papilla.

The exact mechanism for the protruding of the papilla is difficult to determine and probably depends upon a rather complex system of muscles. The longitudinal muscles about the wall of the atrium have processes which attach themselves to the anterior (or ventral) part of the atrium (Fig. 28). At the other end these muscles are continuous with the longitudinal body muscles. Contraction of these muscles of the atrium would have a tendency to widen and to pull forward the anterior part of the atrium. The actual pushing out of the base of the atrium to form the papilla is probably brought about by the numerous diagonal and dorsoventral muscles of the neck region. Contraction of these muscles causing a compression of body tissue in that region would provide a pushing force at the base of the atrium. Once the movement of the extrusion has started, it would be aided by the contraction of the circular muscles in the wall of the atrium and base of the papilla. Of the two specimens with papilla protruded *O. cestoides* showed the ejaculatory duct somewhat coiled even in the papilla itself, while this duct was straight in the papilla of *O. veliporum*. The duct is always coiled between the cirrus sac and the papilla, and in unprotruded papillae. The sudden projection of sperm and seminal fluids through this muscular duct would have a tendency to straighten its coiled condition just as such an effect is brought about by sudden pressure of water in a coiled hose. This influence is, of course, an uncertain one in this case and even if present would probably have a negligible effect in elongating the papilla. The retraction of the papilla doubtless results from the contraction of the longitudinal muscles which it possesses.

The papilla probably functions as a copulatory organ. In the specimen of *O. veliporum* with protruded papilla (Fig. 29), a large mass of sperma-

tozoa was emerging from the genital duct at the tip of the papilla. Spermatozoa were also found crowding the distal tip of the vagina for a short distance, as well as in the genital atrium outside the papilla. None were found in the vagina posterior to the papilla. Eggs were frequently found in the atrium but only when the papilla was completely withdrawn, a fact which indicates that egg laying occurs while the papilla is completely subsided.

The two testes lie one immediately behind the other in the median line at about the center of the body. They are close together and very commonly are in contact with each other. This condition depends, however, upon the state of body contraction. The posterior testis is always slightly larger than the anterior testis. Each testis is surrounded by a fibrous-like membrane containing a few flattened nuclei. In adult forms from the Atlantic collection (*O. cestoides*) the size of the anterior testis was 0.62 to 1.25 mm. by 0.8 to 1.12 mm., while the posterior testis measured 0.8 to 1.37 mm. by 0.8 to 1.2 mm. The organs seemed to be rather consistently somewhat larger in *O. veliporum*.

The duct from the anterior testis leads from the ventral side of that organ near its anterior end, and extends anteriorly in the right half of the body. The other male duct leads from the ventral side of the posterior testis about 1/4 the length of the organ from its anterior end. Thus, in the specimen studied, the posterior testis measured 1.235 mm. and the duct opened 0.365 mm. from the anterior end. This condition may be at least partially due to the angle at which the sections were cut. The duct from the posterior testis leads anteriorly in the left half of the body. Both ducts at first lie ventral to the uterus but like the uterus pass dorsal to the ventral sucker, and in this region they also gradually become dorsal to the uterus. Slightly anterior to the posterior margin of the cirrus sac both ducts swing ventrally. The two do not unite until just before they empty into the seminal vesicle. Relations of the ducts were found to be the same in both *O. cestoides* and *O. veliporum*. Mühlschlag, however, gives the ducts as arising from the median anterior borders of the testes and uniting into a common duct dorsal to the cirrus sac. The diameter of the vas deferens varies but when expanded measures 26 to 39μ with a very thin membraneous wall except in regions where the wall expands into prominent cells. (Fig. 25.)

The cirrus sac is large and elongate-ovoid in shape. It lies between the two suckers somewhat nearer the oral. In average sized specimens (23 to 35 mm.) it measures 0.84 to 1.02 mm. by 0.65 to 0.84 mm. It may attain a length of 1.3 mm. It is somewhat larger in *O. veliporum* where it reaches a length of 1.4 mm. The sac is definitely bounded by a thin membrane about which is an inconspicuous coat of circular muscles. Both seminal vesicle and prostate gland are contained entirely within the sac.

The seminal vesicle is a large swollen tube almost filling the posterior half of the cirrus sac. It is somewhat curved in shape and always packed with sperm cells. The sperm cells are thread-like in form with minute round heads. The wall of the vesicle is made up of flattened cells with large nuclei. The pars prostatica of the male duct leads from the anterior end of the seminal vesicle, proceeds posteriorly and dorsally, then bends anteriorly and runs diagonally forward to the anterior end of the cirrus sac. It is surrounded by the large prostate gland which fills the remainder of the cirrus sac. Just before the duct leaves the cirrus sac its character changes very abruptly into that of the ejaculatory duct.

The ejaculatory duct follows a much winding course leading to the tip of the genital papilla. Distally, it is joined ventrally by the vagina. The coiling of the duct in *O. cestoides* continues in the genital cone itself even when the latter is fully extended. The duct is lined by a thick layer of cuticula-like material continuous with the body cuticula. This layer attains a thickness of 10 to 13μ and shows a folded irregular outline in cross-section. It is surrounded by a thick coat of circular muscles which becomes 20 to 25μ in thickness near the cirrus sac. No longitudinal muscles could be noted.

In development the male reproductive system precedes that of the female. The seminal vesicle is filled with sperm cells some time before eggs appear in the uterus and before the vitellaria appear at all.

The ovary lies immediately in front of the anterior testis and usually in contact with it. In both organs the surface of contact is somewhat flattened. The ovary is therefore flattened on its posterior surface and its longest dimension is in the right and left direction. It may lie a little to one side of the testis, either to the right or to the left. (Figs. 13 to 18.) Its position in this respect is very inconstant and the various descriptions of the position of the ovary in this and similar forms is probably without significance. It is normally almost directly in front of the anterior testis. The size of the ovary in fully mature forms is 0.43 to 0.6 mm. by 0.78 to 0.9 mm. It is slightly larger in *O. veliporum* where it reaches 0.8 by 1 mm.

The ootype lies immediately anterior and slightly dorsal to the ovary with which it is in close contact. Both organs are surrounded by a common fibrous tissue which also separates the two. The ootype is somewhat smaller than the ovary. In an average sized specimen where the ovary measured 0.5 by 0.84 mm., the ootype measured 0.35 by 0.53 mm.

The oviduct leads from the middle anterior aspect of the ovary. It projects into the ovary in the form of a funnel-like structure with thick walls. This condition was found in both species (Fig. 11). The walls are composed of fibrous tissue which is continuous with the tissue covering the ovary and the ootype. This tissue is quite thick between ovary and ootype, and in it occur the two lateral vitelline ducts. As these ducts

approach each other they also tend to encroach upon the ootype so that they give the impression of pushing into it from the rear. Since the fibrous lining tissue becomes very thin between the yolk duct and the cells of the ootype, it is difficult to determine the exact point of penetration of the ootype by the yolk duct on either side. Frontal sections of *O. cestoides* indicate that the lateral ducts may penetrate the ootype before uniting to form the common yolk duct. More commonly, however, the two lateral ducts unite while still within the fibrous tissue close to the ootype and only the common duct actually penetrates into that organ.

Almost immediately after entering the ootype proper the oviduct is joined by the common vitelline duct and by Laurer's canal. The common vitelline duct is very short. A rather unusual condition was found in at least two cases where Laurer's canal instead of joining the oviduct opened at the point of union of the two yolk ducts, so that the three canals opened together into the oviduct (Fig. 24). In other cases noted, Laurer's canal was slightly to the right and appeared to join the right vitelline duct. Again, Laurer's canal may join the oviduct at about the same point as does the common yolk duct.

Laurer's canal is very well developed. It is lined with cuticula 4 to 6μ in thickness. In medium-sized specimens the duct is about 25μ in diameter. A circular layer of muscles surrounds it but no special longitudinal muscles could be made out. The tube is much coiled and leads dorsally and either anteriorly or posteriorly as will be shown later. Within the lumen of the canal are many sperm cells. In some cases, in the region adjacent the oviduct a few yolk cells were noted. A seminal receptacle is absent.

After receiving the yolk duct and Laurer's canal, the oviduct, now the uterus, becomes a small tube only about 26μ in diameter with a thick wall made up of very definite cells with large nuclei. Into the lumen of this tube project cilia-like processes. The tube very shortly enlarges and the nature of its wall becomes one of large cuboidal and heavily granular cells (13 to 23μ in thickness). This part of the tube coils about more or less within the ootype for a short time and continues also outside of that organ.

All stages in formation of the egg shell can be traced from the point where the yolk duct joins the oviduct. The shell material can be first seen as a shapeless irregular mass surrounding an egg cell and a group of yolk cells. Within the cellular-walled uterus region the eggs still lack their characteristic shape. The inner surface of the forming shell often shows vacuole-like spaces (Fig. 26). The cellular region of the uterus as it coils anteriorly soon passes over into a region characterized by a thin simple membraneous wall. By the time the eggs have reached this region they possess hardened and fully formed shells.

The uterus contains thousands of eggs and extends anteriorly in many transverse coils. It passes dorsal to the ventral sucker and ventral to the

seminal vesicle. At about the level of the ventral sucker it becomes less coiled and the nature of its wall changes to produce a region which may be called the vagina.

The vagina like the male ejaculatory duct is lined internally by cuticula. It possesses two layers of conspicuous muscles, an inner circular layer and an outer longitudinal layer. The vagina contains few eggs and above the ventral sucker is almost a straight tube. It leads to near the tip of the genital cone where it unites with the male ejaculatory duct. There is a common duct for a distance of about 25μ.

In development the uterus first appears as a solid string of cells without a lumen. Sections of a very young specimen seem to show a lumen appearing first within the ootype the start of which appears early with the beginning of the ovary. It is an interesting fact that in slightly older specimens when the uterus can first be made out in toto-mounts but before eggs are being produced, this string-like beginning of the uterus assumes the coiling which characterizes the organ when filled with eggs. It winds transversely back and forth between the ovary and ventral sucker, crossing the body as many as 40 to 50 times, approximately the same degree of folding that is found in the adult.

The first eggs to be produced are abortive. A specimen 11.5 mm. in length showed the earliest egg still in the region of the ventral sucker. The most anterior eggs (15 to 20) were only about half the size of the others and were almost spherical with very thin shells. They measured from 22.8 to about 30μ, the smallest being most anterior. The eggs nearer the ovary were larger but still showed a very thin shell, in striking contrast to the thick shell found in the adult egg. No eggs in this specimen measured over 68μ, a measurement slightly below the average adult size.

The vitellaria are interesting because of the variation of their extent and arrangement. They are of the follicular type and consist of separate spherical bodies grouped in two longitudinal rows along the sides of the body. The follicles lie mostly ventral to the digestive system. They do not appear until relatively late in development, or just before eggs begin to be formed. At this time the follicles are very small, approximately the size of the eggs (about 50μ in diameter), but in the adult they reach a diameter of 150 to 190μ. Several hundred of these follicles are connected by ducts which unite into a common lateral duct on each side at the level of the ootype, and these two lateral ducts unite in the ootype as described. The rows of follicles are usually narrow, but the width of the rows often increases to such an extent that the two approach each other medianly. Thus, Miss Lebour (1908) figures the vitellaria massed together posterior to the testes. Such variations are not common, however, the two rows being usually distinctly separate. Irregular breaks or spaces free of follicles are common, and certainly can have no specific significance within the

genus Otodistomum. Even the differences in the vitellaria given by Odhner (1911b) to distinguish *O. cestoides* from *O. veliporum* are quite useless. He gives the vitellaria in *O. veliporum* as beginning behind the middle of the uterus and as being compressed into narrow rows, while in

TABLE 3

VARIATION IN POSTERIOR EXTENT OF VITELLARIA IN *O. cestoides*

Body length *a*	Distance from posterior testis to posterior tip *b*	Extent of right vitellaria beyond posterior testis *c*	Extent of left vitellaria beyond posterior testis *d*	$\frac{b}{c}$	$\frac{b}{d}$
31. mm.	16. mm.	6.4 mm.	7.6 mm.	2.5	2.1
38.	21.	12.8	13.2	1.6	1.5
24.5	13.5	crosses over to left side	7.9	1.7	1.7
20.	8.3	8.3	7.3	1.	1.1
28.	13.5	10.6	9.8	1.2	1.3
17.	7.5	5.6	6.25	1.3	1.2
19.	9.	4.8	3.7	1.8	2.4
29.	14.	both unite in center	8.4	1.6	1.6
38.	18.	9.3	12.1	1.9	1.4
16.	8.	4.6	4.6	1.7	1.7
18.	8.	5.5	7.1	1.4	1.1
16.	6.	both unite in center	5.	1.2	1.2
11.	5.3	2.9	2.9	1.8	1.8
10.5	5.	2.4	3.1	2.1	1.6
10.8	5.	3.3	3.	1.5	1.6
10.5	5.	3.7	3.7	1.3	1.3
11.5	6.	3.9	3.9	1.5	1.5
11.	5.3	2.5	2.5	2.1	2.1
26.	10.5	7.4	7.2	1.4	1.4
26.	14.	united for 2.8 mm.	8.7	1.6	1.6
28.	15.	6.	6.	2.5	2.5
31.	17.	unites with left	7.4	2.2	2.2
28.	13.	unites with left	8.7	1.5	1.5
28.	15.	6.	6.	2.5	2.5
29.	15.	9.4	9.4	1.5	1.5
32.	16.	8.2	10.7	1.9	1.5

O. cestoides the follicles ordinarily begin in front of the middle of the uterus and are not as compressed. This distinction cannot be maintained. In *O. cestoides,* while the vitellaria have their anterior limit between the ovary and ventral sucker, approximately half way between these two organs, they may extend clearly beyond this mid-uterine point or may fail to reach it by some distance.

Posteriorly, the vitellaria always extend considerably beyond the posterior testis and practically always reach at least half the distance

between the hind testis and the posterior end of the body. Two cases (one in *O. veliporum* and one in *O. cestoides*) were noted wherein the vitellaria extended to the extreme posterior tip of the body. One row of the follicles may be several millimeters longer than the other. The rows may unite and run together for several millimeters either medianly or on one side. As such variation in these organs is unusual a table has been prepared to show more detailed measurements (Table 3).

The average egg size for *O. cestoides* was 69.4 by 46.2μ as derived from over 50 measurements. This size agrees with data by Odhner (1911b) who gives 0.065 to 0.072 by 0.043 mm., and Cooper (1915) who gives 0.070 by 0.042 mm. The thickness of the egg shell measured under oil immersion lens averaged about 4.5μ. This thickness is somewhat above the measurements of Odhner, who gives 0.003 mm. and Cooper, who gives 0.0028 mm. The eggs of *O. veliporum* averaged 85.5 by 57.8μ.

GROWTH CHANGES IN *OTODISTOMUM CESTOIDES* WITHIN THE FINAL HOST

Since it is clear that the trematodes must be slightly under 2 mm. in length when first entering the skate, there is a growth within that host to about 40 times. Moreover, the parasite increases its size by six or seven times after it has become sexually mature. This growth of the worm within the skate is marked not only by degree, but also by a regional localization, which results in very different conditions of body proportions in the young and in the adult. The growth is largely in the region posterior to the ventral sucker, and consists mostly in body elongation.

A study was made of this localized growth and its effects upon various body proportions. The material at hand was especially favorable for such study not only because the extremes in size were conspicuous, but also because all intermediate sizes were available.

Regional growth in trematodes has been noted in a general way by various workers. Braun (1894:567) says of trematodes in general: "— junge Exemplare sind nicht nur absolut, sondern auch relativ kürzer, indem besonders das hintre Körperende mit der Entwicklung der Geschlechtsorgane bedeutend an Länge zunehmen kann. Gleichzeitig treten auch andre Veränderingen der Gestalt auf, die so bedeutend sind, dass es oft der Uebergangsstadien bedarf, um eine Jugendform zu diagnosticiren."

As early as 1870 van Beneden stated that the young form of *Dist. hispidium* was entirely different from the adult.

A proportionally greater increase in length than in width was indicated by von Linstow (1890) for *Dist. cylindraceum*, but only a few forms were measured. Specimens measured were 4.5 by 1.4 mm., 6–7 by 1.5 mm., and 13 by 2 mm.

The liver fluke (*F. hepatica*) shows a very marked increase of the posterior regions at the time of sexual maturity as shown by both Thomas (1883) and Leuckart (1886). This growth change also affects the ventral sucker which increases its size ratio to the oral sucker. Thus, according to Thomas (1883:132) the suckers are of nearly equal size in the cercaria while in the adult the diameters of the oral and the ventral suckers have the ratio 1 : 1.35. In *F. hepatica* the body form also increases rapidly in width.

Barlow (1923) gives measurements of hundreds of individuals of *Fasciolopsis buski*. While the size changes in this form are interesting, there does not appear to be conspicuous changes in proportions.

Cort (1921) has given the changes in body proportions with growth in *Schistosoma japonicum*. It is interesting that these changes parallel very closely the changes in *O. cestoides*, an entirely unrelated form. Like the fish trematode, the adult blood fluke is elongate, whereas the young are short and wide. The adult *Schistosoma japonicum* may increase its size as many as 100 times over that of the cercaria. The changes "consist in a very great increase of the length in ratio to the width, an enormous increase of the post-acetabular region of the body as compared with the pre-acetabular, and a gradual assumption of the secondary sexual characteristics which produce the sexual dimorphism of the adult." Especially interesting are changes in the size ratio between the two suckers. "In the cercaria the ventral sucker is only about 1/3 the diameter of the oral sucker. In an early stage of development, the suckers become about equal in size, and in later stages the ventral sucker is constantly larger than the oral sucker." This progressive change in sucker ratio is to be contrasted with the constancy of this ratio in *O. cestoides* as will be shown later.

Growth phenomena have been noticed in the Azygia group by Ward (1910) for *A. sebago* and by Mühlschlag (1914) for *Otodistomum veliporum*. Ward says (of *A. sebago*): "The anterior region assumes the form of an ellipse surrounding the two suckers. This region changes relatively little in size with growth. In one of the smallest specimens (measuring 1.6 mm.) the distance between the centers of the two suckers was 0.5 mm. In one 10 mm. long, this distance measured 1 mm." Mühlschlag found by measuring the largest and smallest specimen of his collection of *Otodistomum veliporum* that the neck region compared with the body region was 1 : 4 in the young forms and 1 : 7.8 in the largest individual. He concludes: "dass bei verschiedener Grösse der Tiere der Hinterkörper relativ stärker wächst als der Vorderkörper."

In *Otodistomum cestoides* the contrast in form between a very young and a sexually mature individual can be seen by comparing Fig. 1 and Fig. 2. Measurements were made on over 200 specimens varying in size from 2.3 mm. to 65 mm. The measurements (taken on alcoholic specimens) included length, width at broadest point, and distance from anterior end to the posterior margin of the opening of the ventral sucker. The margin of the opening was chosen because the outline of the ventral sucker itself is usually not distinct in unmounted specimens. The position of the opening varies somewhat in relation to the outline of the sucker, but, in general, approximates very constantly the true position of the sucker. All measurements can be considered only as approximate as most were taken with a millimeter rule which necessitated estimations of half and quarter millimeters. The smaller specimens were measured microscopically.

The youngest specimens (which very probably represent the earliest condition in the skate) are strikingly unlike the adult in body proportions.

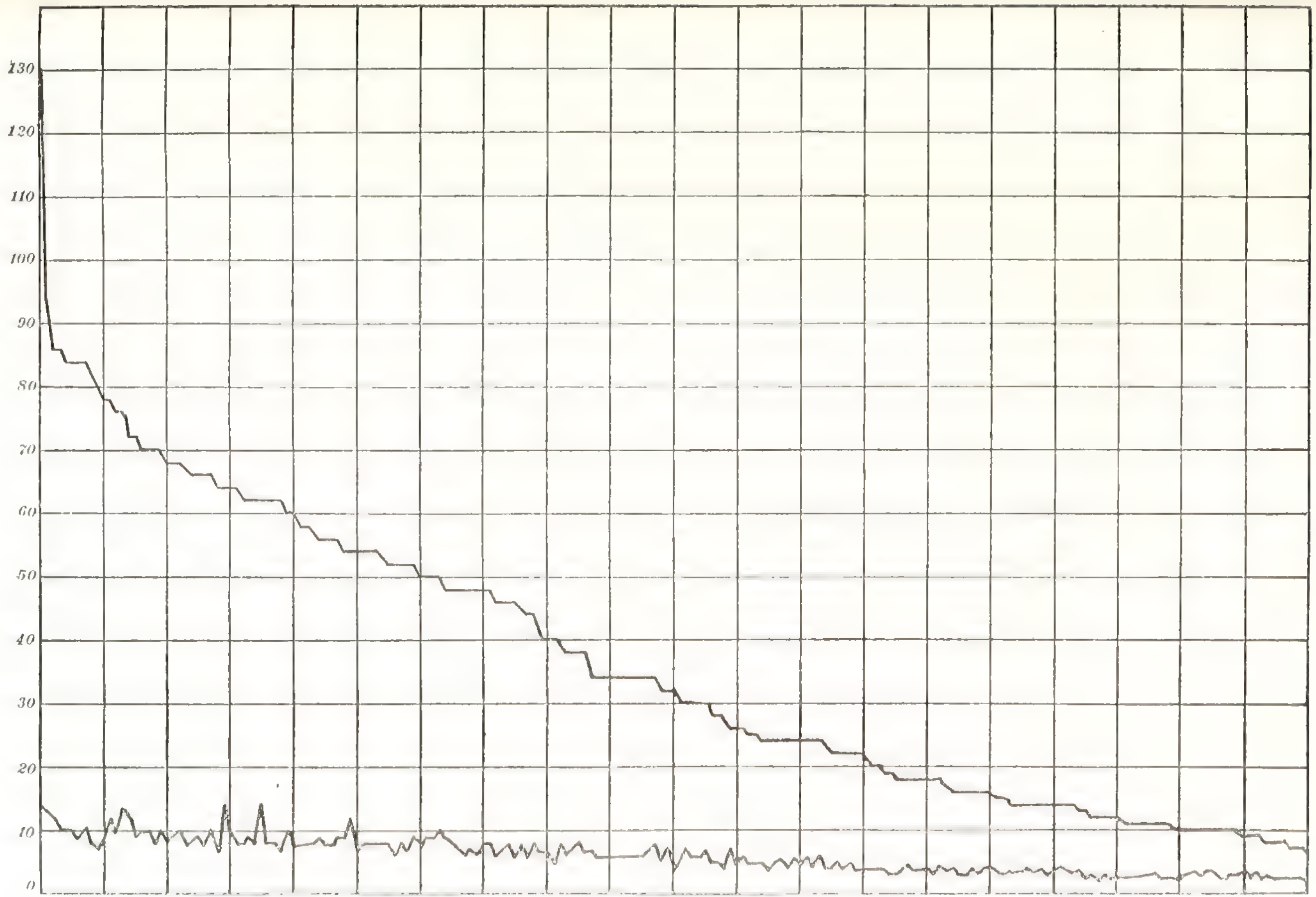

CHART 1. Graphic representation of proportions between total body length and distance from ventral sucker to anterior end in 200 specimens of *Ostodistomum cestoides*.

The base line (0) represents the anterior ends, the upper curve posterior ends of specimens. The lower curve indicates the positions of the ventral suckers. Ten individuals are represented between successive vertical lines. The horizontal lines indicate half-millimeters in multiples of ten.

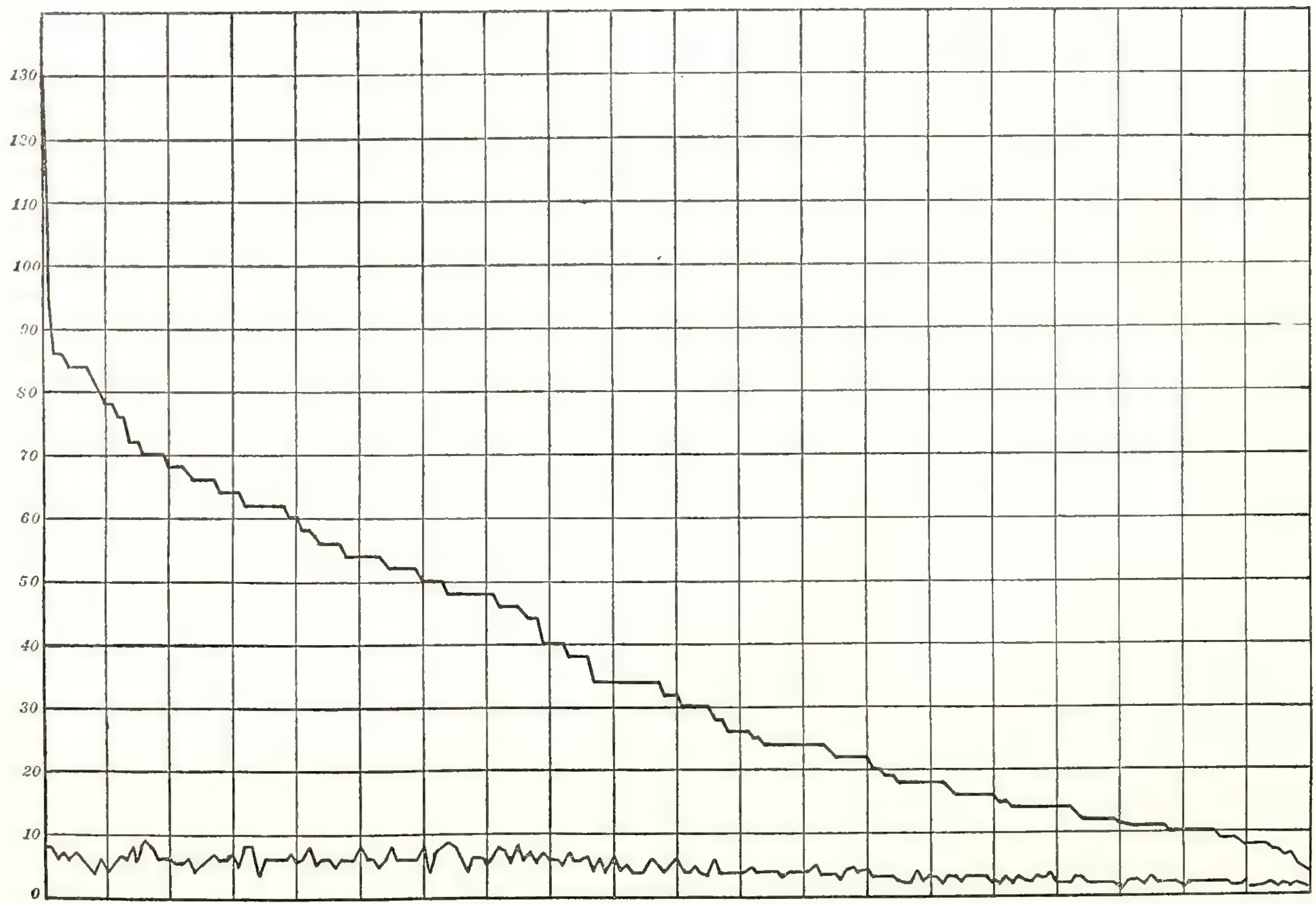

CHART 2. Graphic representation of proportions between total body length and body width in 200 specimens of *Ostodistomum cestoides*. The base line (0) represents the anterior ends, the upper curve the posterior ends of specimens. The widths of corresponding specimens are represented by the lower curve. Ten individuals are represented between successive vertical lines. The horizontal lines indicate half-millimeters in multiples of ten.

Thus, in individuals 2 or 3 mm. in length the ventral sucker is located just anterior to the center of the body, the proportion of the region in advance of the posterior border of the sucker to the entire body length being 1 : 2.3, 1 : 2.5, 1 : 3, etc. (see Chart 1). As the trematodes increase in size, the region posterior to the ventral sucker gradually and constantly gains in size in proportion to the anterior region, which grows relatively little. This change can be followed in the accompanying chart (Chart 1) on which the body lengths and positions of the ventral suckers have been plotted. The total length in half millimeters is plotted on the vertical lines as is also the position of the ventral sucker. Each vertical line, then, represents one trematode so that if the base line be considered as the anterior ends of the worms, the points where the lower curve intersects the vertical lines represent the positions of the ventral suckers, while the upper curve represents the posterior ends of the trematodes. Ten specimens are represented between two successive verical lines. The change in proportion and the constancy of the change can be seen at a glance.

The fluctuations in the lower curve are due to differences in contraction of individual specimens. Because of such differences the chart can only be considered as approximate. Quite a number of the specimens were stretched slightly by hand when killed in order to prevent contraction. Separate tables and charts were prepared, however, for individuals not so treated, and in every case results were the same as in the complete table of all individuals. In the collection of material numerous of the more mature trematodes were destroyed for the purpose of obtaining eggs. Without doubt, the only change which would be caused in the chart by such loss would be to reduce the degree of incline or steepness of the upper curve in the region above horizontal line 50 or 60.

Study of the data on length and width of the trematode at different stages showed corresponding results. The measurements are plotted in Chart 2 where it can be seen that increase in width is very little in comparison with increase in length. The elongate form which gives the adult worm a cestode-like appearance is only gradually assumed with age, and the youngest individuals are very characteristically trematode-shaped. In Chart 2 the distance on any vertical line from the point of intersection of the lower curve to the base line represents the width of an individual specimen whose length is represented by the distance from the *upper* curve to the base line. As the specimens are arranged in order of length, here again all fluctuations due to varying degrees of contraction appear in the lower curve only.

In spite of these radical changes in body proportions, the ratio between the sizes of the two suckers remains constant. That is, the two suckers grow equally evenly, although the body is growing much more rapidly posteriorly.

This constancy of the sucker ratio is somewhat unexpected since other trematodes, especially when body proportions are altered, show an increase of the ventral sucker over the oral. Most conspicuous is the actual reversal in sucker proportion in *Schistosoma japonicum* where, as already given, the ventral sucker is smaller than the oral in the cercaria, but later assumes equality with it, and in the adult is definitely larger. A similar tendency in *F. hepatica* has also been noted.

The following table (Table 4, Column b/c) shows very clearly how all sizes of *O. cestoides* vary closely about the average ratio (oral sucker .66 of the ventral sucker). It is true that in the four smallest specimens is found the largest ratio (up to 0.82), but specimens almost as small show a ratio slightly below (0.64 and 0.65) the average, and some of the largest individuals show a ratio of 0.7 or more.

TABLE 4

SUCKER SIZE IN RELATION TO GROWTH IN *O. cestoides*

Body length (a)	Body width	Diameter of anterior sucker (b)	Diameter of ventral sucker (c)	$\frac{b}{c}$	$\frac{c}{a}$
39. mm.	2.87 mm.	1.43 mm.	2.18 mm.	.65	17.8
38.	2.06	1.25	1.81	.7	21.
38.	2.25	1.312	2.	.66	19.
32.	2.3	1.06	1.62	.65	19.
31.	3.5	1.56	2.18	.71	14.2
31.	2.3	1.3	1.8	.72	17.2
29.	2.75	1.43	2.31	.62	12.5
29.	2.3	1.	1.56	.63	18.5
28.	2.18	1.12	1.75	.64	16.
28.	1.3	1.37	2.	.68	14.
28.	2.18	1.	1.68	.58	16.6
28.	2.87	1.18	1.68	.7	16.6
26.	1.6	.93	1.37	.67	18.9
26.	1.87	1.06	1.37	.77	18.9
24.5	2.37	1.25	1.87	.61	13.
24.	2.8	1.37	2.18	.62	11.
21.	3.1	1.25	1.75	.75	12.
20.	1.68	0.878	1.327	.66	15.
19.	2.12	1.	1.437	.71	13.9
18.	2.5	1.14	1.77	.64	10.1
17.	2.5	1.028	1.77	.57	9.6
16.	2.06	0.916	1.34	.68	11.9
16.	2.5	1.02	1.53	.66	10.4
14.	1.9	1.06	1.5	.64	9.3
13.	2.1	1.5	1.5	.66	8.6
12.	1.8	1.	1.37	.73	8.7
11.5	2.1	0.93	1.5	.62	7.6
11.	1.5	0.75	1.12	.66	9.8
11.	2.1	0.93	1.5	.62	7.3

TABLE 4 (continued)

Body length (*a*)	Body width	Diameter of anterior sucker (*b*)	Diameter of ventral sucker (*c*)	$\frac{b}{c}$	$\frac{c}{a}$
10.8 mm.	1.75 mm.	0.75 mm.	1.25 mm.	.6	8.6
10.5	1.8	0.68	1.31	.52	8.
10.5	1.3	0.68	1.06	.64	9.9
6.5	1.	0.54	0.785	.68	8.3
6.06	1.12	0.525	0.748	.7	8.
5.	0.93	0.448	0.654	.67	7.6
4.5	0.56	0.448	0.654	.67	6.9
4.37	0.9	0.414	0.673	.62	6.5
4.31	1.047	0.504	0.766	.65	5.6
4.18	0.937	0.467	0.635	.73	6.5
4.125	0.991	0.397	0.617	.64	6.6
3.6	0.75	0.414	0.635	.65	5.6
2.37	0.562	0.317	0.43	.73	5.5
2.25	0.748	0.414	0.504	.82	4.2
2.18	0.71	0.355	0.43	.82	5.
1.9	0.56	0.28	0.39	.74	4.8
			Average	.66	

Another interesting point is the relatively much larger size of the suckers in comparison with body size in the young. This observation would follow from the fact that the diameters of the suckers keep pace with the width of the worm. This marked change in proportion between sucker diameter and body length can be followed in Table 4, column c/a. In the smallest specimens, the body length was 4.8 times the diameter of the ventral sucker, while in all the largest specimens measured the body length was about 20 times the diameter of the ventral sucker. The change between these two extremes is seen to be consistent and gradual exactly as was the change body length and width. Young forms in general show the body length to be about 5 times the diameter of the ventral sucker, medium sized specimens have a length about 10–11 times this diameter, while a specimen 38 mm. long was 21 times longer than the diameter of the ventral sucker.

It is interesting to note what effect, if any, the arrival at sexual maturity has upon these growth rates. The uterus is located posterior to the ventral sucker, and it might be expected that the relatively sudden filling of the uterus with eggs would affect growth in this region. The body size at which the trematode attains sexual maturity is quite constant. Almost invariably eggs begin to be produced when the worm has a length of about 11 mm. A few eggs have been found in specimens 10.5 mm. in length. It can be stated quite certainly that sexual maturity is attained between the body lengths of 10 and 15 mm.

Reference to the charts shows 49 specimens between 5 and 10 mm. in length, 30 between 10 and 15 mm. in length, and 22 between 15 and 20 mm. in length. All specimens of these sizes were preserved. As fewer individuals were found intergrading between the sizes 10 and 15 mm. than between 5 and 10 mm., it might be inferred that growth is more rapid in the former case. The indication can only be considered as a slight one, however, as the difference is not large, the numbers are somewhat few, and there is a possibility of various unknown factors such as infection rate.

Further data on the effect of sexual maturity on growth can be obtained by comparing distances from the posterior testis to the ventral sucker (region of uterus) and from this same point to the posterior end of the worm (tail region). At a certain period (11 to 15 mm.) the uterus becomes quite suddenly crowded with eggs. Whether this change alters the proportions of the length of the uterus region to the length of the posterior region where no organs of importance are located, and where no important change is occurring, can be shown approximately by comparing the lengths of these regions in mature and immature specimens. In 21 wholly mature

Table 5

Comparison of Uterus Region with Posterior Body Regions in Young Specimens of *Otodistomum cestoides*

Body length	Length of tail region (*a*)	Length of uterus region (*b*)	$\frac{b}{a}$
14. mm.	6.5 mm.	5. mm.	.7
13.	7.	3.56	.51
12.	6.	3.5	.58
11.5	5.3	3.	.56
11.	5.3	3.	.58
11.	5.25	2.37	.45
10.8	5.	3.25	.65
10.5	4.8	2.87	.6
10.5	5.	2.4	.58
10.	5.8	2.18	.37
6.5	3.25	1.43	.44
6.06	3.	1.47	.49
5.	2.3	1.12	.48
4.5	1.68	1.	.6
4.187	1.68	0.937	.55
4.37	1.5	1.	.66
4.31	1.5	0.75	.5
4.125	1.9	0.687	.35
3.6	1.7	0.57	.34
2.37	1.	0.525	.52
2.18	0.74	0.37	.5
		Average	.493

individuals the length of the uterus region averaged 0.67 the length of the tail region. In 21 immature individuals including a few very young forms, this uterus region averaged 0.493 the length of the posterior region. That is, the uterus region upon becoming filled with eggs increases on the average its ratio to the tail region by about 0.2. While this increase is small, it is very definite. Reference to Tables 5 and 6 shows that the proportion of the

TABLE 6

COMPARISON OF UTERUS REGION WITH POSTERIOR BODY REGION IN ADULT SPECIMENS OF *Otodistomum cestoides*

Body length	Length of tail region (a)	Length of uterus region (b)	$\frac{b}{a}$
38. mm.	21. mm.	12.5 mm.	.6
38.	18.	14.	.77
32.	16.	11.	.67
31.	11.5	9.	.78
31.	17.	9.	.53
29.	14.	9.75	.69
29.	15.	8.5	.56
28.	14.	10.	.71
28.	15.	9.	.6
28.	18.	7.	.4
28.	12.5	10.	.8
26.	11.06	11.06	1.
26.	15.	8.	.56
24.5	13.2	7.1	.53
21.	12.5	6.25	.5
20.	8.	8.	1.
19.	10.	6.5	.65
18.	7.75	5.93	.7
17.	7.5	5.8	.78
16.	6.12	6.12	1.
16.	7.9	4.6	.58
		Average	.67

uterus to the tail region in the young forms measured attained only once a point as high as 0.7 and went as low as 0.34. Moreover, even in these forms the uterus region tended to be slightly greater in individuals with a few eggs (those specimens 10 to 14 mm. in length). Of the mature forms, however, the uterus region was never less than 0.4 the tail region and several times attained equal length with it.

The increase of the length of the body posterior to the ventral sucker over the length anterior to this sucker is by no means due entirely, however, to this seeming increase in the uterus region. To show this fact, measurements of the neck region (that region from the anterior end to the ventral sucker) were compared with measurements of the tail region. The neck

region in 18 immature or recently mature forms averaged 0.77 the length of the tail region, while in 12 mature forms the neck region averaged only 0.39 of the tail region. That is, while the uterus region is gaining on the tail region the latter is also gaining even more rapidly on the neck region (Tables 7 and 8).

TABLE 7

COMPARISON OF NECK REGION WITH POSTERIOR BODY REGION IN YOUNG SPECIMENS OF *Otodistomum cestoides*

Body length	Anterior end to ventral sucker (*a*)	Posterior testis to posterior end (*b*)	$\frac{a}{b}$
13. mm.	3. mm.	7. mm.	.43
11.5	3.5	5.3	.66
11.	3.	5.3	.56
11.	3.	5.25	.57
10.8	2.56	5.	.51
10.5	2.68	4.8	.56
10.5	2.75	5.	.55
6.5	2.12	3.25	.65
6.06	1.5	3.	.5
5.	1.87	2.3	.81
4.5	1.8	1.6	1.1
4.187	1.8	1.68	1.05
4.37	1.87	1.5	1.24
4.31	1.37	1.5	.91
4.125	1.4	1.9	.74
3.6	1.25	1.7	.73
2.3	0.93	1.	.93
2.18	1.04	0.74	1.4
		Average	.77

In stating that the uterus region increases its proportion to the tail region, it has been assumed that the position of the posterior testis is relatively stationary. If, however, the uterus, in filling with eggs, pushes the reproductive organs backward, then the increased growth in the uterus region is only apparent, since the position of the hind testis was taken as a point of measurement. Similarly, illusions would follow from any local movement of the gonads either forward or backward within the body. In general, the gonad group appears to occupy a fixed position. Commonly, especially in extended specimens, the two testes are separate from each other by a short space. When the two organs are in contact with each other the surface of contact becomes flattened. Thus, if the uterus did have a tendency to force the gonads backward, some leeway would be allowed this movement before it exerted an influence on the position of the hind testis, upon which present measurements were based.

TABLE 8

COMPARISON OF NECK REGION WITH POSTERIOR BODY REGION IN ADULT SPECIMENS OF *Otodistomum cestoides*

Body length	Anterior end to ventral sucker (a)	Posterior testis to posterior end (b)	$\frac{a}{b}$
38. mm.	5. mm.	21. mm.	.24
31.	6.	17.	.35
38.	6.	18.	.34
29.	5.	14.	.35
28.	4.	14.	.28
24.5	4.	13.2	.3
20.	4.	8.	.5
19.	3.5	10.	.35
18.	3.	7.75	.38
17.	4.	7.5	.53
16.	4.	6.12	.65
16.	3.5	7.9	.44
		Average	.39

Some slight evidence that the crowded uterus may cause a forcing back of the ovary against the anterior testis is found in certain variations in the relative position of the pore of Laurer's canal. This pore furnishes a fixed point and if it retains a constant position in relation to the ovary in young and in mature specimens, it can be inferred that the position of the ovary is also constant. Such a relation does not exist. The pore was found to be sometimes anterior to the anterior end of ovary, sometimes almost exactly dorsal to it, and sometimes slightly posterior to it. As serial sections were necessary to determine this point, it was ascertained in relatively few cases. In *O. cestoides* the pore was always found to be posterior to the anterior border of the ovary in young or recently mature specimens, and usually anterior to it in mature forms. One exception in both *O. cestoides* and *O. veliporum* shows that the pore may be posterior to the anterior edge of the ovary even in mature individuals. In all young forms measured the pore was posterior to this point. A table follows showing the position of the pore in specimens of different ages:

O. cestoides

Length	Maturity	Pore in relation to anterior end of ovary	Distance
10 mm.	uterus with few eggs	Posterior	0.56 mm.
Small	immature	"	0.18
Small	only a few eggs in uterus	"	0.23
14 mm.	Recently mature	Anterior	0.14
25 mm.	Mature	"	0.18
Large	Mature	"	0.18
Large	Mature	Posterior	Slight

O. veliporum

23 mm.	Mature	Anterior	0.6 mm.
25 mm.	Mature	Posterior	0.285

In any case, the extent of this shifting as far as it is indicated by relative pore position is not sufficient to affect materially the position of the hind testis. Conclusions in regard to growth changes can be more graphically expressed by means of a diagram (Diagram 1).

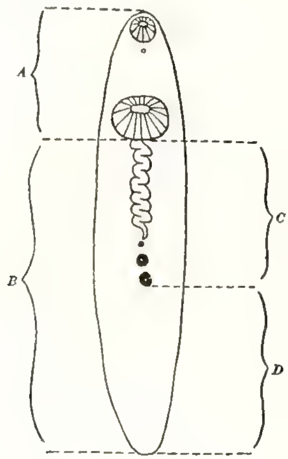

DIAGRAM. 1. Diagram to show growth changes in *Otodistomum cestoides*. Distance B constantly grows faster than Distance A, even before sexual maturity. Distance C increases slightly its proportion to D after sexual maturity. Distance D increases in length more rapidly than A, even after sexual maturity. Body length increases much more rapidly than body width. Size ratio of the two suckers does not change with size of the worm. Suckers are proportionally much larger in young.

COMPARISON OF *OTODISTOMUM CESTOIDES* AND *O. VELIPORUM*

The close resemblance of these two species has already been noted. Odhner (1911b) gives the following differences:

	O. veliporum	*O. cestoides*
1.	Size: 50 mm. by 5 to 6 mm.	Size: to 65 mm. by 3 to 5 mm.
2.	Ratio of suckers: 3 : 5	Ratio of suckers: 3 : 4
3.	Vitellaria beginning behind the middle of uterus field, compressed into narrow bands.	Vitellaria usually beginning in front of middle of uterus field, not so narrowly compressed.
4.	Egg: 0.86 by 0.06 to 0.063 mm.	Egg: 0.065 to 0.072 by 0.043 mm.
5.	Thickness of egg shell 0.006 mm.	Thickness of egg shell 0.003 mm.

Of these differences, numbers 2 and 3 are certainly useless as all conditions involved were commonly found in the present studies of the single species, *O. cestoides*. Odhner placed importance on the thickness of the egg shell.

Mühlschlag (1914) worked on *O. veliporum* and concluded that the following features separate it from *O. cestoides*: (1) its body is less in length, greater in width; (2) its eggs are larger, and (3) have a much thicker shell. He found that the thickness of the egg shell of *O. veliporum* to reach 7μ or more than twice as thick as commonly reported for *O. cestoides*.

The trematode from *Raia binoculata* from the Pacific has already been frequently compared with *O. cestoides* from the Atlantic "barn-door" skate. It has been seen that the Pacific form presents very few significant differences. Chief among these differences is the egg size. The average egg size from over 50 measurements in the Pacific form gives 85.5 by 57.8μ as compared with 69.4 by 46.2μ in *O. cestoides*. This difference is real, constant, and significant. In no case did the egg size overlap between the two species. Thus, the eggs in the Pacific form agree almost exactly with the reported egg size for *O. veliporum*.

One of the other reported differences between these two species is a slightly greater body width in *O. veliporum*. The average width of 75 Atlantic specimens (*O. cestoides*) between 23 and 50 mm. in length was 3.22 mm. The average width of 65 Pacific specimens (*O. veliporum*) between the same length limits was 3.81 mm. Thus, again the Pacific form agrees with descriptions of *O. veliporum*. The Pacific specimens were quite constantly of greater thickness, however, and their slightly greater width might be due to an average higher degree of body contraction.

The only other specific criterion to be applied is the thickness of the egg shell. *O. veliporum* supposedly possesses a much thicker egg shell than

does *O. cestoides*. In this particular, the Pacific form studied does not agree with the published records for *O. veliporum*. An average of numerous measurements on the egg shell gave a thickness of about 4μ. For *O. cestoides* an egg shell thickness of about 4.5μ was found. Thus, instead of having an egg shell twice as thick as does *O. cestoides*, the Pacific form actually has a slightly thinner egg shell. Measurements were taken on mature eggs in distal regions of the uterus. The eggs nearer the ovary had a slightly thicker shell. Even though this discrepancy in egg shell thickness appears to be a constant feature in material studied, it hardly seems to be in itself a specific character. In the first place, the absolute difference in egg shell thickness between the Atlantic form and records for *O. veliporum* is slight (about 2μ) since the Atlantic material showed an egg shell somewhat thicker than recorded for *O. cestoides*. Again, such minute measurements are difficult to determine exactly, especially as slightly oblique sections through the egg exaggerate the apparent thickness of its shell. Finally, the constanty of this feature is not well established, as is, for example, egg size in this genus.

In respect to other differences noted between the two forms, the condition of the genital atrium and papilla has already been discussed and showed to be unreliable as a specific character. It can only be said that, in general, the genital papilla was either absent or small in size in *O. veliporum*, and usually prominent and robust in *O. cestoides*. It may, however, be flattened out entirely in *O. cestoides* and entirely protruded in *O. veliporum*.

The genital organs seemed proportionally somewhat larger in *O. veliporum*. Actual measurements (in millimeters) on specimens of approximately similar size are as follows:

O. cestoides				*O. veliporum*			
Length 32 mm.	Testis (ant.)	0.9 by	0.87	Length 32 mm.	Testis (ant.)	1.25 by	1.25
	" (post.)	1.	0.81		" (post.)	1.5	1.25
	Ovary	0.43	0.81		Ovary	1.	0.75
31	Testis (ant.)	0.68 by	0.9	30	Testis (ant.)	1. by	0.9
	" (post.)	0.8	0.9		" (post.)	1.27	1.
	Ovary	0.5	0.68		Ovary	0.8	1.
24	Testis (ant.)	0.89 by	0.37	25	Testis (ant.)	1. by	0.89
	" (post.)	0.78	0.86		" (post.)	1.3	0.89
	Ovary	0.46	0.7		Ovary	0.8	0.6

A 39 mm. specimen of *O. cestoides* agreed more nearly with the 32 mm. specimen of *O. veliporum* in gonad size, as follows:

39 mm.	Testis (ant.)	1.25 by	0.87 mm.
	Testis (post.)	1.37	0.9
	Ovary	0.6	0.9

These differences in gonad size are not, however, sufficient to be significant. Miss Lebour (1908) figures very large gonads for her species which was clearly *O. cestoides*.

From this study, it has been concluded that the Pacific material represents *Otodistomum veliporum*. Furthermore *O. veliporum* and *O. cestoides* are shown to be even more similar than has hitherto been pointed out. The most certain distinction is found in egg size. *Raia binoculata* (=*R. cooperi*) is a new host for *O. veliporum*.

O. veliporum (Creplin) has the following synonyms:

Dist. veliporum Creplin
Dist. insigne Dies.
Dist. microcephalum Baird — according to Ariola 1899
Dist. scymni Risso
Fasc. squali grisei Risso
Dist. veliporum of Johnstone 1902

It has been recorded from the following hosts: *Notidanus griseus*, *Notidanus cinereus*, *Echinorhinus spinosus*, *Carcharias milbertii*, *Raia batis*, *R. clavata*, *R. fullonica*, *R. radiata*, *R. lintea*, *R. binoculata*, *R. stabuliforis* (=*R. laevis*), *Scymnus nicaeensis*, *Acanthias vulgaris*, *Carcharias* sp., *Laemargus melanostoma*, *Scyllium canicula*, *Chimaera monstrosa*, *Carcharias rondeletti*, *Centrolophus pompilus*.

THE MIRACIDIUM OF *OTODISTOMUM CESTOIDES*

[FIGS. 31–43]

The first larval form or miracidium of *O. cestoides* was studied from live material and in toto-mounts. As the larva is well developed and ready to hatch when the eggs are laid, sections of eggs in the vagina formed the basis for study from sections. Many thousands of the eggs can be obtained by cutting the adult worm just beneath the ventral sucker and pressing out the eggs in the distal portion of the uterus. This method gives a mixed culture of eggs of various degrees of maturity. A more uniformly mature collection results from saving only the eggs from the vagina region. Unsuccessful attempts were made to secure eggs that had been normally laid. Adults were kept both in sea-water and in sea-water with mucous and fragments from the stomach of the host. In the latter case, some specimens were kept alive two or three days, but in no case were any eggs obtained. There is no reason to believe, however, that the eggs in the vagina do not represent the normal condition of the eggs when laid.

The eggs can be readily hatched. They were kept in sea-water in vials surrounded by running sea-water. The water in the vials was changed twice daily. The eggs were found to be very hardy. In mixed cultures containing many immature egg stages, hatching larvae appeared most frequently only after 7 to 10 days. In the case of cultures of only the most mature eggs, several miracidia were observed only 5 hours after the eggs had been removed from the worm. This very early hatching shows that the larva is fully developed in the egg at the time of oviposition. In general, even when the eggs in a vial seemed quite uniform, no uniform period of hatching was observed. Only a small proportion of the eggs hatched, and these hatchings, few at a time, extended over periods of some days (up to 15). The large number of cultures undertaken gave ample opportunity of studying the rather peculiar miracidium.

The youngest immature eggs are pale yellow in color and quite transparent. They average only slightly smaller than mature eggs and the thickness of the shell seems to be about the same at all stages (in *O. cestoides*). In the early stages the embryo consists of only a few cells collected at the opercular end of the shell, while the rest of the space is occupied by numerous yolk cells. These latter gradually disappear as the embryo grows, until the egg shell seems to contain a uniform mass of cells.

The more mature eggs while alive have a characteristic appearance. The shell is brownish-yellow in color. A few small, globular bodies are

scattered about within the shell while at one end, the anterior, a dark opaque granulated area appears, concealing the anterior tip of the embryo. This area thins out posteriorly so that a dark crescent-shape appearance is given (Fig. 31). The same condition is described by Leuckart (1886:380) for *D. lanceolatum.* Just posterior to this area and within the body of the embryo are two conspicuous, hump-like structures continuous anteriorly, but of two parts (resembling lobes) posteriorly. What was probably a similar structure was seen and pictured by von Nordmann (1832) for the eggs of *D. rosaceum* (=*Azygia lucii*). It represents a conspicuous organ of the embryo. Nordman noted the bifid character of the organ, describing it as "eine gleichsam zusammengekrummte, dunkler begrenzte Figur, welche an einem Ende wie mehr oder weniger gespalten ershien." All subsequent descriptions of the larva of *A. lucii* consider the organ as simple, sac-like in structure and it has been interpreted as representing a simple type of intestine. In one case, in eggs of *O. cestoides* the body appeared to be split into three rounded lobes (Fig. 32). Even while the embryo is still in the egg, a more or less circular lighter area can be made out within the "lobes" of this organ, an appearance suggesting the presence of a lumen in each. The *Hüllmembran* of Schauinsland (1883) can be found in stained material. It is a thin membrane containing a few flattened cells. It is left behind in the egg shell at time of hatching.

The miracidium is non-ciliated and normally pear-shaped, with a narrow anterior region. Its shape is continually changing, however, as the worm-like movement of the larva results in alternate expansion and contraction of the body. When at full length the shape is narrow and elongate, reaching a maximum of 90 to 100μ; when fully contracted the body becomes spherical and about 45 to 50μ in diameter. The posterior end is sometimes pointed. The anterior end of the larva is pulled in and pushed out simultaneously with the contraction and extension of the body. The action of this narrowed anterior region is exactly like that of a proboscis. The earliest movement noted within the egg can only be described as an indefinite "squirming." At no time is there any indication of ciliary movement.

The process of hatching was observed several times. At this period, the movement of the larva has become very definite and like that of the free miracidium, consisting of the alternate pulling in and pushing out of the somewhat pointed anterior end. The movement results in a series of pushes or blows directed at the operculum which sooner or later opens and the worm slides out. The ease of hatching seemed to vary considerably. Thus, one case was observed when the entire process of hatching required only about 30 seconds and almost without effort on the part of the embryo. Another case studied showed a very active embryo which did not succeed in hatching even after several hours and finally its movements slowed down and ceased. Focusing showed that this animal did not seem to be accurately

oriented in the shell and the force of the propulsion of the proboscis was directed a little to one side of the operculum. Although there was ample space for the worm to change its position, it seemed to persist in directing its "blows" at one spot. With the escape of the embryo from the shell, a small stream of minute granules is also given out. These particles attracted small infusorians in the culture and sometimes an empty egg shell would be well filled with small ciliated protozoa.

The body of the miracidium is covered by a very thin cuticula-like layer which is non-ciliated. About the anterior end is a region of bristles or spines. Such an occurrence of spines is common in non-ciliated miracidia. In *Azygia lucii* they are described as occurring on four plates (Borstenplatten) surrounding the anterior end of the larva. This Azygia larva also has a posterior series of four bristle plates. Although Odhner (1911b) states that "Borstenplatten" are not present in the genus Otodistomum, the spiny areas were very conspicuous in living material. They were also discernible in toto-mounts and could occasionally be definitely made out in sections of embryos within the eggs. Unlike their condition in *A. lucii*, these bristles occur on five strips or areas radiating from the anterior tip. Each strip is tapering in form, being broadest posteriorly. The bristles are longer near the tip and gradually become shorter posteriorly. When the larva first hatches these strips or plates of bristles lie quite flat. Very soon, however, they become loosened at the anterior end and peel off backwards. This shedding of the bristle-plates often gives to the miracidium a very peculiar appearance, as the strips remaining attached posteriorly resemble appendages. The strips are of a very thin epiderm-like material, and when free from the larva tend to curl slightly (Figs. 34 and 43). The process of shedding the strips can be compared in a homely way with the peeling of a banana.

Creutzburg (1890) in his work on the life history of *Dist. ovocaudatum* (=*Halipegus ovocaudatus*) which has a larva very much like that of *O. cestoides*, found that the miracidium of that species lost its coat of bristles only after it had pierced the intestinal wall of a snail. While he does not mention any localized areas of the bristles he describes the shedding of the epiderm as proceeding from the head end. He says (p. 22) the embryo "verwandelt er sich, ... durch Abwerfen der äusseren stacheltragenden Bedeckung, deren Loslösung nach meinen Beobachtungen zunächst am Kopfpol vor sich geht. . . . ." It is therefore quite possible that the spiny region normally serves to aid the miracidium in piercing the tissues of the host. In my material, only one live individual was seen which seemed to have completely shed the bristle plates.

Larvae were usually closely associated with the empty egg shell from which they emerged. The posterior end of the larva seemed to show a tendency to adhere to the egg shell. Only a few larvae were seen at any

great distance from their egg shells. Locomotion was certainly very limited and even the most active larvae progressed very little, if any, in the watchglasses wherein they were studied. The anterior end seemed to adhere rather tenaciously to any debris with which it came in contact (Fig. 34).

The only conspicuous organ of the larva is the structure already mentioned as visible in later egg stages. It extends to about the middle of the body and has a paired sac-like appearance. In one favorable specimen it was observed that leading forward from this organ is a minute duct which opens at the extreme anterior tip of the larva. This anterior tip when free from the bristle-plates is rounded and knob-like in shape. The rounded lighter areas in the central part of each of the lobes of the organ have the appearance of lumens, and the impression gained from study of live material is that the entire organ represents a bi-lobed or bifid intestine. Such a conclusion is supported by the fact that many miracidia have been described as possessing a simple type of intestine. Furthermore, what is certainly the same structure in similar larvae (miracidia of *A. lucii*, *H. ovocaudatus*), has been commonly interpreted by Looss, Leuckart, Creutzburg, Schauinsland, and others as an intestine.

Stained material, and especially sections through mature eggs, present evidence which seems to warrant questioning very seriously the conclusion that this organ represents any form of intestine. In the first place, the organ is found to consist not of two parts but of four. The outline of these "lobes" or parts stains with hematoxylin clearly. The bifid appearance is explained by the fact that the four parts are arranged in pairs (Figs. 36 and 38). The elements of a pair are closely associated, but the pairs may be wide apart (Fig. 38).

Furthermore, the central region (of each lobe) which had been interpreted as a lumen, invariably stains darkly like a nucleus. The granular appearance of the organ in life disappears in sections and in its place is seen a clear transparent area. Safranin staining gave results similar to those obtained with various hematoxylin stains. In fact, safranin stains brought out the four-partite and four-nucleate condition even more clearly than hematoxylin.

The fact that the organ is made up of four similar parts, and that the central regions stain like nuclei make it seem more probable that the organ is not an intestine but a group of unicellular glands. One bit of evidence in favor of viewing the organ as an intestine has been the reported occurrence of a minute pharynx or muscular region about the duct. Only the slightest suggestion of such a structure was detected in the present studies although no special staining of live material was attempted. Von Linstow (1890) reports what appears to be a similar structure in *D. cylindraceum* as a "Stutsapparatus." Schauinsland (1883), however, describes and pictures

a minute pharynx-like structure in the larvae of *Azygia lucii* and other trematodes. He does not hesitate to consider such a structure as a true pharynx and the sac-like organ as an intestine. It is interesting to note that in no case does he show any form of cellular structure around the so-called intestine, nor does he show that any lumen is present. On the contrary, he does represent nuclei-like bodies within the intestine in *A. lucii* larvae. It is quite evident that these are the same type of bodies which stain like nuclei in my sections. Schauinsland refers to them as "Kerne im Darminhalt." In one case, he reports "Im Darm bemerkt man 3 Kerne." Both for the larva of *A. lucii* and for the larvae of the other forms he studied, Schauinsland shows from one to four nuclei within the contents of the intestine.

Looss (1894) shows the same condition in his figures. Particularly interesting is his figure of the larva of *A. lucii.* Here three rounded bodies are clearly present within the organ interpreted as an intestine. In the present studies Azygia material was found to be most favorable in sections of *A. acuminata.* Here were found four apparent nuclei within the organ in question (Fig. 44). The organ seemed to be simple and sac-like in shape. Because of the much smaller size of the larvae in Azygia species it would be very difficult if not impossible to make out the four-partite condition which the larger larvae of Otodistomum reveal.

The miracidium of *Schistosoma japonicum* possesses in addition to a sac-like intestine with four nuclei, a pair of large "cephalic glands," one gland being located on each side of the intestine. The glands are nearly as large as the intestine. The four-partite condition found in *O. cestoides* showed, however, no such differentiation between the parts.

Creutzburg (1890) has given not only a description of the appearance of this organ in the similar larva of *Halipegus ovocaudatus* (=*D. ovocaudatum*), but also a history of its fate in later development. In the larva he studied, the organ seemed to be simple and sac-like in form. He says (p. 21): "Dieser körnige Inhalt zeigt oft bläschenähnliche Einschlüsse, die auf das Vorhandensein eines Lumens schliessen lassen." This larva (which does not hatch until the egg has been eaten by a snail) penetrates the intestinal wall of the snail. Soon after it has passed into the body cavity of the snail the larval "intestine" or organ in question begins to diminish in size and finally disappears. Creutzburg says (p. 21): "Die weitere Entwickelung des schlauchförmigen Organs lässt sich noch bei den Sporocysten verfolgen, wo es, seine ursprüngliche Lage am vordern Körperende beibehaltend, späterhin an Grösse allmählich abnimmt, und schliesslich ganz verschwindet." Creutzburg himself was somewhat uncertain as to the correct interpretation of the organ, but in view of its similarity to so-called intestines in other miracidia he concluded it represented a rudimentary intestine.

The conception of an intestine implies the presence of a cellular wall and a lumen. In none of the above instances has either of these conditions been demonstrated. That the organ in question might be interpreted as a group of uni-cellular glands seems more justified. This latter view would be more in accord with the nuclear-like content noted in present material and also described by Schauinsland and others. It would also explain the four-partite condition shown in Figures 36–38 and 40–41. These divisions of the organ into more than two parts seem to offer the strongest evidence against its interpretation as an intestine. Furthermore, if the possible glandular secretion served to aid penetration into the intermediate host, the gradual disappearance of the organ after this act was accomplished in the case of *H. ovocaudatus* would be explained. The tendency showed by the larvae of *O. cestoides* to cling to debris at their anterior ends will be recalled.

While it is true that the miracidia of many trematodes require no glandular secretion in order to penetrate their host, yet it should also be remembered that most miracidia are strongly ciliated and an effective boring force is attained by the action of the cilia which supply a constant forward pressure. On the other hand, the propulsive force of the miracidia-form under consideration is quite different in that when the force is directed against an object the entire body of the larva tends to be pushed backward. As the contents of the intestine of a snail are probabily less resistant than the intestinal wall, the physical power of unciliated miracidia would seem to be less effective in this first tissue penetration than is such power in ciliated miracidia.

Unciliated miracidia of digenetic trematodes are very rare. Except among the Azygiidae they are definitely known only in *Halipegus ovocaudatus*. Von Siebold as early as 1837 described an unciliated miracidium for *Dist. variegatum* (later *Dist. cylindraceum* = *Haplometra cylindracea*) but later workers disagreed with this conclusion. Schauinsland (1883) found the larva to possess a coat of cilia which it shed at time of hatching. Von Linstow (1890) found that the shedding of the ciliated coat was due to premature hatching, and that the larva is normally free-swimming. Willemoes-Suhm (1871) described the miracidium of *Ptychogonimus megastomus* and showed it to be very similar to Otodistomum larvae, possessing bristle plates and no cilia. The non-ciliated larvae of *Azygia lucii* and *Halipegus ovocaudatus* have been best known. Leuceruthrus now remains the only genus of the Azygiidae whose miracidium has not been studied.

NOTES ON THE LIFE HISTORY OF *OTODISTOMUM CESTOIDES*

The very thick shell of the egg in *O. cestoides* indicates that these eggs possess the capacity for waiting a long period of time before hatching. On the other hand, the mature larva within the egg at the time of oviposition shows that under favorable conditions the egg may hatch immediately. The further fact that the miracidium lacks the power of locomotion indicates that the eggs do not normally hatch until eaten by a snail. Schauinsland (1883) believes that such is normally the case for *Azygia lucii*, the eggs of which he found hatching in the intestine of a snail. Leuckart (1886:66–67) says that this condition is probably true for all unciliated miracidia. He states: "unter den Arten mit glatter Embryonalhaut scheint es doch manche zu geben, die im Wasser entweder gar nicht oder doch nur selten ausschlüpfen, vielmehr solches vermuthlich erst dann thun, wenn sie, noch umschlossen von der Eischale, in den Darm eines geeigneten Trägers gerathen sind. So sah ich die Embryonen des *Distomum ovocaudatum* niemals im Freien ausschlüpfen, obwohl ich die schon im Mutterleibe vollständig sich entwickelnden Eier wochenlang, bis zum Absterben, im Wasser cultivirte. Eine ähnliche Beobachtung machte Schauinsland an *Dist. tereticolle*, dessen Embryonen im Darme von *Lymnaeus palustris* und *L. stagnalis* noch nach 24–36 Stunden lebhaft umherkriechen, aber im Wasser nur selten frei werden."

The larvae of *Halipegus ovocaudatus* after hatching in the intestine of the intermediate snail host develop into sporocysts as shown by Leuckart and Creutzburg. The explanation of the ready hatching of the eggs of *O. cestoides* in sea water is found in the effect of the changes in concentration of the sea water due to evaporation. This effect was accidentally discovered when a culture of mixed eggs was left exposed in a watch glass for several hours. Evaporation of the sea water caused the opercula of the eggs to open whereupon the larvae, even though immature, partially escaped. The same result was repeatedly noted when sea water containing eggs was allowed to evaporate. The more mature eggs hatch more readily and the larvae appear active and healthy. When the evaporation is pronounced the less mature eggs open and the embryos partially slide out from the shell. Embryos thus prematurely hatched show no movement. Young eggs wherein the body form of the embryo is not definitely established do not open. In regular cultures the evaporation was slight and gradual, so that only mature eggs were stimulated to hatch.

Still further evidence that the eggs do not normally hatch in a free state is furnished by the following data: Three vials of fresh eggs were covered with an animal parchment membrane and immersed in a large aquarium of running sea water. Here any change of concentration due to evaporation would be negligible. Although all of these cultures were examined at intervals for about a week, no hatched eggs or larvae were found, while eggs collected at the same time but kept in open vials hatched with customary regularity. This experiment to eliminate evaporation was tried with the purpose and hope of increasing the hatching of the eggs. The fact, however, that this more normal environment of the eggs reduced or eliminated hatching is in full accordance with the later discovered cause of hatchings by evaporation of the sea water.

The opening of the operculum of the egg shell therefore seems to be induced directly or indirectly by an increase in density or osmotic pressure in the surrounding medium. The indication is that the stimulus is primarily a physical one rather than a chemical one. That is, increased density in the content of the snail's intestine as compared with the density of sea water, rather than any chemical peculiarity of the location within the snail, induces the hatching of the eggs. This conclusion receives support from Schauinsland's experiments in hatching the eggs of *A. lucii*. He obtained normally laid eggs, and found that the speed of their hatching could be greatly increased by placing them in a solution of common salt. In this solution the eggs hatched in about 15 minutes or practically immediately. It seems clear that no particular chemical substance is necessary for the stimulation to hatch, but merely an increase in osmotic pressure in the surrounding medium. Whether such a stimulus to hatch is direct or indirect is, of course, unknown. It is possible that the discrepancy in densities within and without the egg shell stimulates a secretion from the gland cells of the embryo, and that this secretion is the direct cause of the opening of the operculum. Some evidence in favor of this possibility is seen in the fact that even excessive evaporation does not cause the younger eggs to open although the operculum is well defined in the one-celled egg stage.

Various molluscs common in the vicinity of Frenchman's Bay were kept in vials of egg cultures. After periods varying from about 12 hours up to several days, these molluscs were removed and examined microscopically by means of smears. In general, all of this work was unsatisfactory. Eggs retained between the shell and body of a snail showed a tendency to hatch after the snail had been out of water for some time. This result would be expected, being probably due to sea water evaporation. There was no evidence that larvae so hatched penetrated the tissues of the snail. Unfortunately, during most of the work, no special examination was made for the presence of eggs in the intestine. One very conspicuous case was

discovered, however, when it was found that *Littorina litorea* ate these eggs very readily. Pellets of fecal or food matter in the intestine showed eggs present in large numbers. The snail had been kept for four days in a vial containing eggs. One pellet from the intestine contained over 50 eggs, another 25, 15, 12, etc., down to 4 or 5. A live larva was found by lightly crushing one of these pellets under a cover glass. The location and condition of this larva leaves no doubt that it had recently hatched from one of the eggs in the intestine of the snail. The snail had been dry and out of water for about a day and a half. Two out of six other specimens of Littorina examined by smears showed eggs in the intestine. This condition was further investigated by examination of serial sections of snails exposed to eggs. All of four specimens of Littorina so sectioned showed numerous eggs in the intestine. These eggs sometimes occurred in large numbers (several hundred). One case of a partly hatched larva was discovered in these sections. Careful examination revealed no certain case wherein such larvae had penetrated the wall of the intestine. Serial sections of two specimens of *Thais lapillus*, one of which had been in a very vigorous culture for over a week, gave practically negative results. Occasionally, isolated eggs were found in the digestive tract of one of these specimens, while the other contained no eggs. Sections of *Buccinum undatum* (which had, however, been in the egg culture only one night) showed no eggs.

An encysted distome was not uncommon in both Littorina and Thais, but it could not be determined as Otodistomum. It occurred in thin walled cysts near the digestive tract. Redia and cercaria were also found in these snails, but probably those discovered did not belong to Otodistomum. No definite conclusions can therefore be drawn in regard to the first intermediate host, except that some species of snails (especially Littorina) readily devour the trematode eggs, and that these eggs can hatch in the intestine of the snail. Other species of snails under similar conditions seem to eat very few or none of the eggs.

In the meantime, rather conclusive evidence has been found in regard to the last intermediate host of this trematode, at least in European waters. Scott (1909), in his report on fish parasites of Scotland waters, states in his discussion of *Dist. cestoides*: "Several young specimens of a Distomum, which closely resembles the immature *D. cestoides* from the skate, were found encysted on the walls of the stomach of a Witch Sole, *Pleuronectes microcephalus*, captured in Moray Firth. There were several cysts observed, and all those examined contained only young Distomids—in some cases one, in others two examples.

"Fishes form a considerable proportion of the food of large skates, and probably the Witch Sole, which lives in moderately deep water, sometimes becomes the prey of these large Plagiostomes."

Nicoll (1913a) records *Otodistomum cestoides* (van Ben.) from *Raia macrorhynca* and adds the following: "In regard to the life history of this species, it is probable that the cercaria discovered by Scott, encysted in the stomach wall of the witch, *Pleuronectes cynoglossus* (in Scott's paper this species is inadvertently named *P. microcephalus*) represents the larva of *O. cestoides.* In the same fish I have found encysted in the wall of the stomach a cercaria, which from its large size and general structure, cannot be referred to any other species. It occurred as a large orange-yellow globular cyst 1.95 mm. in diameter, firmly attached to the outer wall of the stomach by a short pedicle. The wall of the cyst consisted of a thick, tough outer coat within which was a large amount of viscous yellow material. The cercaria measured 2.4 mm. in length, with a maximum breadth across the ventral sucker of 0.66 mm. Both suckers were transversely elongated, the oral measuring 0.29 by 0.35 mm. and the ventral 0.43 by 0.59 mm. The latter was situated at a distance of 0.96 mm. from the anterior end. The pharynx was small and situated close to the oral sucker. There was a very short esophagus and wide diverticula extending in a slightly sinuous manner to the posterior end of the body. The excretory vesicle was Y-shaped and consisted of a median stem extending a quarter of the length of the body, and two lateral branches reaching forward as far as the pharynx. No other organs were visible."

This cercaria described by Nicoll resembles almost exactly my youngest forms from the skate. A copy of Nicoll's figure is given for comparison (Figures 2 and 3). As Nicoll points out, no other trematode is known to which this cercaria could belong except *O. cestoides.* Reference to my records shows that the sand dab and flounder are among the most common fish food of the big skate. No cysts were found containing cercaria, but relatively few of these flat fish were examined. It is very probable that the sand dab or flounder conveys the trematode to the big skate. The degree of infection and range of size of the parasite in the skate indicating a continuous infection is in accordance with this conclusion.

The immature trematode found encysted in the stomach wall of *Lophius piscatorius* and named "*Xenodistomum melanocystis*" by Stafford appears to be an immature *O. cestoides.* It is so identified by Odhner (1911b), who concludes that the goose-fish does not represent a true intermediate host, but that the cysts in that host represent an accidental infection.

SYSTEMATIC REVIEW OF THE FAMILY AZYGIIDAE

The characteristics of the family Azygiidae as given by Odhner (1911b: 513–14) are as follows:

Mehr oder weniger langgestreckte und abgeplattete "Distomen" mit einem derben, muskelkräftigen Körper von 5–75 mm. Länge. Saugnäpfe sehr kräftig entwickelt, einander genähert. Haut unbewaffnet, mit dicker Cuticula, die sich beider Kontraktion in unregelmässige Querfalten legt. Darm mit kräftigem Pharynx, äusserst kurzem Oesophagus und bis ins Hinterende reichenden Darmschenkeln; ein Präpharynx fehlt. Excretionsblase Y-förmig mit sehr langen, bis ins Kopfende reichenden (und sich dort mitunter vor dem Mundsaugnapf vereinigenden) Schenkeln. (Bei Ptychogonimus ist der Hauptstamm sehr verkurzt.) Genitalporus median, zwischen den Saugnäpfen. Die charakteristische Entwicklung der Endteile der Geschlechtsweg biëtet die beste Bürgschaft für die nahe Verwandtschaft der in diese Familie zusammengestellen Gattungen: der Genitalsinus ist sehr geräumig entwickelt; die männlichen Leitungsweg bestehen aus Ductus ejaculatorius, Pars prostatica und Samenblase, die beiden letzteren schlauchförmig und ausser bei Ptychogonimus von einem Cirrusbeutel umhüllt; die ganze Komplex liegt unmittelbar vor oder über dem Bauchsaugnapf. Ovar und Hoden median, unmittelbar hintereinander in Hinterkörper gelegen. (Ausnahme: Leuceruthrus.) Uterus von Ovar aus nach vorn ziehend (Da er bei Ptychogonimus vor dem Ovar zuwenig Platz für seine Entfaltung findet, sendet er jederseits zwischen den Geschlechtsdrüsen und Dotterstöcken eine lange Schlinge nach hinten bis in die Nähe des Hinterendes). Laurerscher Kanal vorhanden, Receptaculum seminis fehlt. Dotterstöcke follikulär entwickelt, in den Seiten des Hinterkörpers, nicht bis ins äusserste Hinterende reichend. Vagina vorhanden. Eier etwa 0.045–0.085 mm. lang, gedeckelt; sie enthalten bei der Ablage ein reifes, anscheinend immer unbewimpertes Miracidium.—Magenparasiten bei Fischen.

Odhner included the following genera in this family: Otodistomum, Azygia, Leuceruthrus, and Ptychogonimus. Azygia and Otodistomum are the most nearly related genera. Leuceruthrus has a very different arrangement of gonads, and Goldberger (1911:7) suggested that it might represent the type of a new family. In this genus the testes are lateral and anterior, being far removed from the median and more posterior ovary. Odhner, however, shows that this forward migration of the testes is of secondary importance, compared with the similarity which the genus shows to Azygia in the character of the genital atrium. Ptychogonimus shows the most marked deviations from the family type. These deviations lead toward certain characteristics of another group of marine trematodes known as the Distomum-clavatum group. Consideration of this relationship might be of value in determining the systematic position of the family Azygiidae.

Trematodes of the *Dist. clavatum* group are also of large size with powerful, muscular bodies, and are found in the stomachs of marine fish. The group, containing a number of species, has been an isolated one

taxonomically. In 1911, Odhner placed the group as a sub-family of the Hemiuridae. Although designating these forms as of sub-family rank, he did not give a sub-family name. Nicoll (1915) in his list of trematodes of British fish, classified them under the Accacoeliinae. The term "Dist. clavatum group," although awkward, is curiously persistent. The species in question (*Dist. clavata* (Menz.) Rud.) is actually *Hirudinella clavata* as designated by Blainville in 1824. Blainville later included also in this genus the former *Fasciola ventricosa*. The forms have been usually referred to the genus Distomum. All species in the group probably belong to the genus Hirudinella.

Similarities of this group to the Azygiidae in general are: large size, muscular bodies, no pre-pharynx, very short esophagus, similar excretory system, and similar genital atrium. This latter condition forms a very important and striking resemblance. Jägerskiold (1900) describes the genital sucker of *Distomum megastomum* (=*Ptychogonimus megastomus*) as "ein neuer Typus von Kopulationsorgenen." He compares the terminal genital regions of *D. veliporum*, *D. clavatum*, *D. verrucosum*, and *D. megastomum*, and offers the suggestion that the latter (which now represents the genus Ptychogonimus) is phylogenetically derived from a form resembling *D. veliporum* through a series now represented by members of the *Dist. clavatum* group. This suggestion is based solely on comparison of the "Kopulationsorganen." The comparison does show that so far as the distal genital apparatus is concerned, Ptychogonimus is more similar to the Hirudinella group than to the genera of the Azygiidae. This similarity is marked not only by the more conspicuous folds and muscle rings in the wall of the atrium, but also by the fact that both sex ducts open separately on the genital papilla in Ptychogonimus and in Hirudinella.

The lack of a cirrus sac in Ptychogonimus is another important feature in which that genus is like Hirudinella and different from other Azygiidae. Furthermore, the uterus in Ptychogonimus sends two coils posterior to the ovary and extending nearly to the posterior end of the body. This distribution of the uterus is unlike anything found in other Azygiidae but very similar to the condition in Hirudinella.

Odhner's distinction between the Azygiidae and the Hirudinella group is that in the latter not only have the testes migrated forward (as in Leucerthrus) but the ovary has followed also. The ovary is then located directly behind the testes instead of in front of them as is the normal condition in the Azygiidae. He continues (p. 524): "—dadurch werden also die Lagebeziehungen zwischen Ovar und der Hauptmasse des Uterus die umgekehrten zu denen der Azygiiden. Nach diesem zweifellos recht schwerwiegenden Merkmal habe ich in erster Linie die Familiengrenze gezogen."

However, as two coils of the uterus extend posteriad in Ptychogonimus, in this genus also the chief mass of the uterus is posterior to the ovary as can readily be seen from the figures of Jacoby (1899). One of the chief distinctions, then, between this genus and the Hirudinella group seems to be the position of the ovary in relation to the testes. Yet the significance of gonad location was discounted by Odhner himself when he included Leuceruthrus in the Azygiidae. Ptychogonimus, however, possesses follicular vitellaria as in Azygia, and not tubular as in Hirudinella. Again, its body is flattened and less muscular than Hirudinella. Considering these latter features, the genus is probably more appropriately considered as a member of the Azygiidae. Yet evidently it shows a relationship between the two groups and through it the family Azygiidae leads to the Hemiuridae and to a sub-family near the Accacoeliinae.

The miracidium of Ptychogonimus is non-ciliated and bears a spiny anterior region as does the miracidium of Azygia. Odhner considers Ptychogonimus to be more closely related to Azygia than to Otodistomum "namentlich auf Grund des Baues der Miracidien." It has, however, already been shown that Otodistomum larvae are also equipped with bristle-plates. This inference of relationship between genera on the basis of larval forms is interesting. No description of the miracidia of Hirudinella species could be found, but, judging from sectioned material of *Hirudinella fusca*, the mature eggs in this species do not contain larvae at all similar to those contained in mature eggs of Otodistomum. Hence, the first larval form of Ptychogonimus probably relates that genus more closely to the Azygiidae than to Hirudinella, *if* similarity of larval forms is reliable evidence. But there is reason to believe that similarity in miracidia of different species does not necessarily indicate close specific or even generic relationship of the adult trematodes. Thus, the miracidium of *Halipegus ovocaudatus*, a parasite of the frog, has the very same morphological features that characterize the miracidia of Azygia and Otodistomum. It is of the same shape and movement, is unciliated, possesses bristle plates, and has the so-called "intestine" (Creutzberg, 1890). Yet the adult form of Halipegus is not closely related to Azygia. The natural explanation is that the adults have undergone evolution independently of their larval forms. The non-ciliated miracidium is probably always associated with the fact that the egg normally hatches only after eaten by a snail. The retention of this feature in developmental history results in the retention of a certain type of larva. In the meantime, the adults (in the two cases cited) seem to have evolved along different lines without change in their miracidia. That is, one finds here the very common condition of constancy of larval forms and divergence of adults. The other possibility of convergence of larval forms is not probable in this case because the miracidia resemble each other in such great detail.

The genera of the Azygiidae can be separated by the following key:

Uterus sending coils posterior to ovary........................Ptychogonimus
Uterus entirely anterior to ovary
  Ovary and testes more or less directly behind one another in median line
    Genital pore close to acetabulum, branches of excretory system separate..................................Azygia
    Genital pore nearer oral sucker, branches of excretory vesicle united anterior to oral sucker............Otodistomum
Testes lateral and anterior to ovary..........................Leuceruthrus

Ptychogonimus has the single species *megastomus*. *Leuceruthrus micropteri* is the only representative of the genus Leuceruthrus.

The two species of Otodistomum have already been considered at length. The egg size is the most certain distinction between them.

Eggs averaging about 69 by 46μ........................*O. cestoides*
Eggs averaging about 86 by 58μ......................*O. veliporum*

A key to the species of Azygia will follow later.

Azygia is the only genus of the family showing taxonomic confusion in its species. As it is morphologically very similar to Otodistomum, some of the difficulties leading to confusion were encountered in the present studies, and led to further comparative study of different species of Azygia as well as of the two genera themselves. These difficulties involved the question of relative significance of such factors as: body size and shape; extent and arrangement of the vitellaria; relative size and position of the suckers; shape of pharynx; position of gonads; and size of eggs.

In the first place it is important to note that these forms are all very muscular and highly contractile. Their nature in this respect can be contrasted with such forms as Dicrocoelium and Opisthorchis, so that even though the internal arrangement of organs may be similar, the heavy muscular body sharply distinguishes the Azygia group from them. Looss noted this fact in 1899 when he pointed out that the common descriptions of *A. lucii* (=*Dist. tereticolle*) hardly separated it from the genus Opisthorchis. Yet Opisthorchis is a delicate, quite muscularless form, and not closely related to Azygia.

Body contraction in the Azygia group where the worms are elongate in form not only alters the general shape, but it also changes the relation of the ovary and testes so that the former may lie almost lateral to the anterior testis, instead of directly anterior to it. In spite of the fact that Goldberger (1911) noted this variation in his *A. acuminata*, he nevertheless separated his genus "Hassalius" upon this condition. The genus Hassalius has already been rightly reduced to synonymy with Azygia by Odhner (1911b) and by Ward (1917). Moreover, body contraction results in throwing the intestinal ceca into folds, giving them a zig-zag appearance.

Such an appearance is entirely without significance except as it indicates to some extent the degree of contraction. It should be eliminated as a distinction between species. A pointed or blunt caudal region is also a character depending largely upon temporary body contraction.

Some confusion among genera and species is also due to a rather extreme range in size exhibited by the trematodes of this group. The conspicuous growth of *Otodistomum cestoides* even after arrival at sexual maturity, has already been considered. While this feature is common among trematodes, it seems to be particularly prominent in Azygia species. Odhner is therefore justified in considering Stafford's genera, Megadistomum and Mimodistomum (which were largely based on body size) as synonymous with Azygia.

The extent and arrangement of the vitellaria are often very constant in trematodes. In the Azygiidae, the vitellaria are less reliable for specific diagnosis than might be expected. The variability of these organs in *O. cestoides* has been noted in detail. Odhner allows them almost unlimited range in Azygia species also. Certainly the importance given to details of these organs by Goldberger has been unwarranted. In the present studies, the constancy of the vitellaria in the various forms was critically studied, and will be considered in connection with the different species.

One histological feature of special interest in highly muscular trematodes such as the Azygiidae, is the arrangement of body muscles. Body muscles in trematodes usually consist of certain layers (circular, longitudinal, and diagonal) immediately beneath the cuticula. In addition to these muscle layers of the body wall, there occurs in the present group a well developed layer of longitudinal muscles within the parenchyma. These muscles running parallel with the longitudinal muscles of the body wall occur in bundles forming a more or less compact layer, so that in cross-section there is separated a central region containing most of the organs from an outer cortical region. Ward (1910) called particular attention to these muscles in *Azygia sebago*. They were also described and figured by Leuckart (1886) for *Azygia tereticolle*. Concerning them Leuckart (p. 18–19) says: "Unterhalb des Hautmuskelschlauches ordnen sich diese Parenchymfasern hier und da wieder in förmliche Schichten, wie z.B. bei *Distomum tereticolle*, bei dem sich in einiger Entfernung von den Diagonalmuskeln der Rinde eine scharf begrenzte zweite Längsfaserschicht bildet, die aus kräftigen Spindelzellen besteht und mit Ausschluss der Dotterstöcke die in dem hellen, von Bindegewebe erfüllten Zwischenraum zwischen ihr und dem Hautmuskelschlauche zu liegen kommen, sämmtliche Eingeweide in sich einschliesst." Thus, the vitellaria occurred outside the muscles, as Ward found for *A. sebago*. In the present study of different American forms of Azygia, the vitellaria always occurred outside this muscle layer. The

available sections of Goldberger's *A. acuminata* showed the muscles less developed and more widely scattered.

The occurrence of similar body muscles in Otodistomum serves as an additional histological link of relationship between these forms and Azygia. Villot (1879:7) describes the grouping of such muscles for *D. insigne* (=*Otodistomum veliporum*). He says: "Une dernière couche de fibres longitudinales disséminées dans la zone limite du parenchyme. Ces fibres sont très-fortes." Villot's figures clearly show these muscles as a definite layer. They represent a condition similar to that found in Azygia species, but their position is distinctly different in Otodistomum where they completely enclose the vitellaria. My own studies on *Otodistomum cestoides* and *O. veliporum* show the muscles present in a discernible layer but more scattered than in Azygia species, and external to the vitellaria.

What may represent a homologous arrangement of longitudinal muscles has also been described for trematodes of the *Hirudinella clavata* (=*Distomum clavatum*) group. These forms are extremely muscular and contractile. In the neck region of *H. clavata* the following muscle layers occur: circular layer, longitudinal layer, oblique layer, and finally another internal zone of longitudinal muscles. Concerning this latter, Poirier (1885:483) says: "Celle-ci se compose d'un grand nombre de faisceaux musculairessouvent très gros, et formés de fibres longitudinales d'un fort diamètre." Poirier describes a rather peculiar condition posterior to the ventral sucker. In this region, he says (p. 484): "toutes les zones de fibres musculaires à l'exception de celle des faisceaux longitudinaux internes, ont complètement disparu. Cette dernière, par contre, a pris un développement considérable. Elle est formée de faisceaux composés d'un grand nombre de fibres, très serrés les uns contre les autres, de facon à former une gaine épaisse, à peu près continue, à l'antérieur de laquelle se trouvent le parenchyme du corps et les différents organs de l'animal."

I have found (in agreement with Mühlschlag, 1914) a similar condition in *Hirudinella fusca*. The other body muscles, however, do not here completely disappear as recorded by Poirier. Throughout the body length in this form there occur from the cuticula inward the following muscle layers: (1) circular, (2) longitudinal, (3) circular, (4) longitudinal. Layer (2) is always very weak with only scattered fibers. In mid-body region, layer (4) is very powerful with heavy fibers grouped in large bundles. It is this inner layer which is possibly homologous with the internal parenchyma muscles of Azygia and Otodistomum. It differs from them in being immediately surrounded externally by a ring of circular muscles. Granting that these muscles are present in all three groups, they differ in Azygia species by being located *internal* to the vitellaria, whereas in Otodistomum and Hirudinella they are found *external* to the vitellaria.

The writer has been fortunate in obtaining for study type or original material of all the different Azygia forms described from America with the exception of those recorded by Stafford. Co-type material of *Azygia perryii* Fujita from Japan was also studied. The conclusions reached will be included under the following discussions of accepted species.

AZYGIA ANGUSTICAUDA[1] (STAFFORD 1904)

[Fig. 27]

Synonyms: *Mimodistomum angusticaudum* Stafford 1904
Azygia loossii Marshall and Gilbert 1905
Azygia loossi Odhner 1911

The descriptions of the two above mentioned forms appeared at about the same time. Since in the present work material was obtained only of *A. loossii*, the distinctive specific characters will be taken from that material. Goldberger (1911) has redescribed this species at some length. Reference to Stafford's description will be made a little later.

The position of the gonads in the extreme posterior region of the body seems to be a point in which *A. loossii* is distinct from all other species. In this form the testes are located about 1/7 to 1/8 the body length from the posterior tip. Furthermore, the ventral sucker in this species is only slightly anterior to the middle of the body, whereas in other species it is distinctly more anterior. Such marked differences could possibly be explained by a highly extended anterior region and a highly contracted posterior region. But in the few specimens available, it was very clear that the entire body was extended. The uterus in *A. loossii* appears to be tubular with eggs in linear order, but this condition may be due to the possibility that the specimen had but recently arrived at sexual maturity. The musculature of the genital atrium seems to be particularly well developed in this species, so that the genital pore appears to be surrounded by a small sucker. The eggs average about 52 by 28μ which is intermediate between the recorded sizes of eggs in *A. sebago* and *A. acuminata.*

What seems to be an additional important feature of this species is the extent of the vitellaria almost to the region of the ventral sucker. Although the vitellaria actually begin in the mid-body region instead of anterior to it as is common in other species, the fact that the ventral sucker itself is equatorial in position explains the relative proximity of the vitellaria to it. The proportion of body length to distance from ventral sucker to most anterior vitellaria was found to be 27.2 and 26.2, a ratio reached only by *A. acuminata.* (See Table 18.) *A. loossii* was collected

[1] Due to an obvious misprint the name of this species was spelled "augusticaudum" in Stafford's original paper.

from *Micropterus salmoides*, *Lucius lucius*, and *Amia calva* from Wisconsin lakes.

The above characters do not seem to warrant a new genus for this species, as in every important respect it agrees with the genus Azygia. It seems quite certain, however, that it does represent the same form described by Stafford as "*Mimodistomum augusticaudum*" from the mouth, pharynx, esophagus, and stomach of *Lota maculosa* and *Stizostedion vitreum*. Stafford describes the ventral sucker "as situated in the middle of the length of the worm in the most normal cases. The genital glands are flattened against each other and crowded backwards near to the ends of the caeca." Comparing it with Azygia, he says: "In the 12 mm. Azygia I selected as example, the ventral sucker is 2 mm. from the anterior end. In the 7 mm. Mimodistomum it is 3.5 mm. from the end, while the relatively long distance between sucker and ovary is in marked contrast to the short distance between the latter and the posterior end of the worm."

Thus, although Stafford's description is brief, the differences he points out are exactly those between *A. loossii* and other American species. That is, there is no point in Stafford's description of "*Mimodistomum angusticaudatum*" that does not agree with *A. loossii* and practically every point mentioned is characteristic for that species. If, therefore, Stafford's description is to be accepted there seems to be no escape from considering the two species synonymous.

AZYGIA ACUMINATA GOLDBERGER 1911

[Figs. 21, 22]

Goldberger unfortunately emphasizes unimportant points (*e.g.*, vitellaria unbroken, ceca zigzag, tail pointed, constricted neck region) in distinguishing this species. A study of his material, together with specimens of the same species collected and identified by Cooper, has led to the belief that this form represents a true species capable of distinction by definite features. A few specimens* from Dr. Ward's collection from the same host (*Amiatus calvus*) apparently also belong to this species.

Certain similarities in all of the material could be demonstrated. The constriction of the neck just anterior to the ventral sucker appears to be fairly constant and noticeable. This character should not be emphasized, however, as Goldberger's own figure of his *Azygia bulbosa* shows that some slight localized and temporary constriction may occur in this region in other species. The most distinguishing specific characters were found to be: relatively wide body, anterior extent of the vitellaria, egg size, and poorly developed condition of the internal parenchyma muscles. It should be realized that the nature of all of these features is of somewhat precarious

* Collection of Dr. H. B. Ward, vials Nos. 25.27 and 25.28.

standing in this genus. Probably no one of them, unless very marked, would justify a recognition of a separate species. Only because of the general association of all of these characters can the forms be separated from the other common American species. It may also be of some significance that all of the material is from the same host, *Amiatus calvus.*

The proportion of body width to body length can be seen in Table 15. This point cannot be considered a reliable specific character. Generally speaking, *A. acuminata* usually shows a wider body than most of the other forms.

In nearly every case, the vitellaria began at about the level of the posterior edge of the ventral sucker, rarely appreciably posterior to it. In none of the other American species was this general condition found except in *A. angusticauda* (Staff.) wherein this matter has already been discussed. Table 18 compares *A. acuminata* with the other forms in this respect.

The average egg size of twenty measurements from Cooper's specimens was 64.8 by 28μ. The average egg size of about fifty measurements from Goldberger's specimens was 63.4 by 34μ. The egg size in Ward's material was 63 by 29μ. All of these averages are considerably above the egg size of the most nearly related Azygia species (Table 14). This large size is attained in the largest specimens of a few forms (like Leidy's *Dist. longum*), but was never found in specimens of sizes similar to *A. acuminata.*

Four sectioned specimens (three from Goldberger's material, and one from Cooper's) agreed in showing a much more scattered and less compact

TABLE 9. *Azygia acuminata*
Measurements in millimeters

Length	Width	Oral sucker	Ventral sucker	Post. edge v. sucker to mid. ovary	Post. edge v. sucker to ant. end	Post. edge v. sucker to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
8.*	1.68	1.	0.75	2.6	3.3	0.4	1.37	0.31	0.31
11.3*	2.5	1.3	1.		3.9	0.65	2.56	1.56	0.96
10.9*	2.5	1.3	0.93	3.4	3.87	0.37	2.5	0.63	1.01
9.75*	1.3	1.	0.68	3.3	3.1	0.5	2.4	0.5	1.5
*	2.5	1.25	1.		3.87	0.74			
9.68*	2.5	1.3	1.	3.	3.75	0.3			
9.87*	2.6	1.25	1.06	3.56	3.62	0.35	1.4	0.65	1.15
6.87	1.8	1.18	0.9	1.9	2.5	0.	1.6	0.78	0.84
6.56	1.75	1.06	0.74	2.3	1.75	0.5	1.6	0.95	0.76
6.3	1.5	0.93	0.78	2.	2.18	0.	1.4	0.84	0.13
7.5	2.	1.18	1.	2.68	2.75	0.	1.68	0.88	1.03
8.87†	1.4	0.87	0.812	2.93	3.3	0.3	2.18	1.5	1.56
9.37†	1.3	0.87	0.812	3.75	3.3	0.75	2.18	0.87	1.18
11. †		0.93	0.75	3.87	4.12	0.5	2.8	1.87	1.9

arrangement of internal, longitudinal parenchyma muscles than was found in the other Azygia species.

Table 9 (page 60) gives measurements of the available *A. acuminata* specimens. Those marked * were collected by Cooper; those marked † are from the Ward collection and were obtained at Fairport, Iowa, in 1916 by T. B. Magath. In each case the host was *Amiatus calvus.*

Pearse (1924) records *A. acuminata* from the "wall-eyed pike" in Lake Pepin, Wisconsin, but gives no further data.

AZYGIA LONGA (LEIDY 1851)

[Figs. 19, 20 and 30]

Synonyms: *Dist omum longum* Leidy 1851
Dist omum tereticolle of Leidy 1851
Megadistomum longum (Leidy) Stafford 1904
Azygia tereticolle of Stafford 1904
Azygia sebago Ward 1910
Azygia bulbosa Goldberger 1911
Hassallius hassalli Goldberger 1911
Azygia lucii of Cooper 1915

Authentic material of all these forms (with the exception of Stafford's) was obtained. A careful comparative study of this material has led to the acceptance of the above list of synonyms. The occurrence of intermediate conditions between somewhat extreme types, and the high degree of variability of some factors, necessitates the extension of the limits of the species as will be shown. In view of the high degree of contractility and marked growth changes of trematodes in this group, all comparisons were made relative to body length and on the basis of body proportions. Even on this basis consideration must be given to relative changes in proportions with growth.

Azygia sebago Ward (1910) from the Sebago salmon is the best described of American species. Leidy's *Dist. longum* reported in 1851 and the various other species recorded from America since 1910 have appeared to differ more or less markedly from *A. sebago.* These differences will now be critically examined.

In separating *A. sebago* from the European species, *A. lucii* (=*A. tereticolle*) Ward emphasized the posterior extent of the vitellaria. Although Odhner (1911b) is partially justified in discounting dependence upon vitellaria in this genus, the distinction seems to be a valid one. Not only in *A. sebago,* but in all American forms of Azygia examined, the vitellaria always extend appreciably beyond the hind testis, usually at least half way from this point to the posterior end, and may even reach to the extreme posterior tip as was observed in one case. According to descriptions and figures of *A. lucii,* the vitellaria end in the region of the hind testis and

rarely extend appreciably posterior to it, although van Beneden (1858) says the vitellaria reach "depuis la ventouse posterior jusqu'en dessous du second testicule." His figures show the vitellaria extending beyond the hind testis to a point about 1/4 the distance between that organ and the posterior end. Looss (1894:16) describes their extent for the European species as follows: "Die Dotterstöcke erstrecken sich in den Seitentheilen des Leibes ausserhalb der Darmschenkel nach vorn hin nicht bis an den Bauchsaugnapf—sie endigen ungefähr die Länge seines Durchmessers vorher-, nach hinten zu kaum jemals bis über hintere Grenze des zweiten Hodens hinaus."

Further distinction between American species and *A. lucii* can probably be found in pharynx shape, a point upon which Odhner separates a new species, *A. robusta*. The pharynx of American species is more globose than the elongate pharynx of *A. lucii*. This point will be considered in more detail under *A. robusta*.

A. sebago averages about 6 to 8 mm. in length. Specimens were found as small as 1 mm. and no ova were present in forms 2.85 mm. long. In regard to sucker proportions: "The ventral sucker or acetabulum is usually distinctly smaller than the oral. In the extreme case it appears about equal in size or, on the other hand, only about half as large" (Ward, 1910:1177). The questions of body size, size at sexual maturity, egg size, and sucker proportion are important points of comparison in American Azygia species.

Of the other Azygia species, *A. bulbosa* Goldberger is most evidently identical with *A. sebago*. The descriptions of the two forms show no important differences. Type material of both species was studied. Reference to comparative tables (Tables 15 to 18) shows almost identical body size and proportions, as well as similar position and arrangement of organs. Goldberger gives the egg size of *A. bulbosa* as 56 by 25μ. Although the eggs may reach a length of 57μ, the average of my 110 measurements gave the egg size as 48.3 by 28.7μ. Ward gives the egg size of *A. sebago* as 48 by 27μ.

The original type material of *Hassallius hassalli* Goldberger was also examined for comparison. That all of this material was strongly contracted was made very evident by the ring-like foldings of the cuticula and the excessive foldings of the intestine. Goldberger himself explained the "numerous transverse sulci" of the cuticula as "apparently due to contraction of the worm." The high degree of body contraction is also evidenced by the longitudinal compression of the organs, especially the uterus, gonads, and vitellaria. The pharynx is brought down closer to the ventral sucker than is normal. Yet, in spite of the evident body contraction, Goldberger separates his genus from Azygia on a thicker, shorter body form, and a lateral position of the ovary in relation to the anterior testis, both of which characters would be caused by body contraction. The only

comparison Goldberger makes between the two genera is in these words: "This new genus, aside from its external characters, differs from Azygia in the position of the ovary, which here is by the side of, that is in the same transverse plane as the cephalic testis, instead of cephalad of the latter as in Azygia." The shorter and thicker body shape is directly due to contraction. In regard to the position of the ovary, reference need only be made to Goldberger's figure of *Azygia acuminata* (his Fig. 8) and to the following sentence from his description of this Azygia species: "In one of four press preparations, the ovary bears exactly the same relation to the testes as that in *Hassallius hassalli;* that is, it is within the zone of the cephalic testis." In Azygia species as in Otodistomum (see Figs. 13–18), the ovary may be located slightly to the right or to the left of the anterior testis, and is consequently forced into the "zone"of this testis when the body is contracted. Until the ovary can be shown to be lateral to the testis in uncontracted specimens, this character cannot be given even specific significance.

In fact, after allowance is made for body contraction, this form cannot be distinguished from the other common American forms as represented by *A. sebago* and *A. bulbosa.* Goldberger's own description and figures show the terminal genital apparatus in his *A. bulbosa* and *Hassallius hassalli* to be exactly similar. Study of his publication and original material reveals not a single point of difference between the two forms, except differences that might be due directly to body contraction. Comparison of sagittal sections of this species with sagittal sections of *A. sebago* and the *A. lucii* of Cooper shows no differences that can in any sense be considered specific. Goldberger gives an egg size of 48 by 26μ measured from sections. My measurements of eggs from toto mount gave about 49 by 24μ, but the larger eggs measured from sections were from 54 to 57μ in length by about 24μ in width, or practically exactly the measurements for *A. bulbosa.* The internal parenchyma muscles in *Hassallius hassalli* are prominent and are exactly as in *A. sebago* and the *A. lucii* of Cooper.

Leidy in 1851 described *Distomum longum* from the mouth of *Esox estor* (=*E. lucius*). Stafford (1904) designates as "Megadistomum longum Leidy" forms which he collected from the mouth, esophagus, and stomach of *Esox masquinongy.* These trematodes are very long, Leidy's specimens being up to 76. mm. (3 inches) in length, while Stafford reports living worms as extending to 127. mm. (5 inches), a truly prodigious length. Stafford gives a normal length of 75 mm. Both Leidy and Stafford give the oral sucker as slightly larger than the acetabulum. Odhner (1911b) expresses the view that this trematode should be considered as a large Azygia species. Cooper (1915) collecting material from *L. masquinongy* considers his form the same as that reported by Stafford and identifies it as *Azygia lucii.*

Study of Leidy's original *Distomum longum* and Cooper's material clearly shows that they represent members of the genus Azygia. Their large size is certainly not sufficient basis to warrant Stafford in forming a genus, Megadistomum. Leidy's *Dist. tereticolle* (from *Esox reticulatus*) also was compared with them, and in the single specimen available in the Leidy collection, the oral sucker, contrary to Leidy's description, was found to be slightly larger than the acetabulum. In *Dist. longum*, Leidy describes the genital opening as "just anterior to the middle of the neck, or nearer the oral acetabulum." Such was not the condition in the two specimens of this form available. In each case the genital aperture was close in front of the ventral sucker, as is, indeed, characteristic of the genus Azygia. In the most elongate specimen the esophagus was unusually extended longitudinally and at its base a swollen region showed a marked resemblance to the cirrus sac. It is possible that Leidy mistook this appearance for the end-apparatus of the genital system. The true position of the terminal genital-apparatus in *Dist. longum* is seen in Figure 30.

Cooper also collected Azygia species from the pike (*L. lucius*). These latter trematodes were much smaller in size, and apparently a different species, but Cooper, after a careful comparison of his smallest examples from the maskinonge with those from the pike, concludes that they represent a single species. He also points out the highly variable size at which egg production begins. A 14. mm. trematode showed less mature eggs than one 6. mm. long from the same host. "On the other hand," Cooper adds, "examples of intervening lengths may have their uteri distended with ripe eggs!" (Cooper 1915:192). Forms from the trout were all immature although they reached a length of 11 mm.

This variable size at which eggs are first produced in Azygia species is in contrast with the fairly constant size at sexual maturity in Otodistomum species. The large number of different hosts in which Azygia species occur may be associated with this variability. Another possible factor is the season of the year, but the influence of this factor would be difficult to determine. Eleven different fish hosts have been reported for the present Azygia species. Ward collected his material in July and August and found that those forms from the smelt although attaining a length up to 11 mm., were always immature. Cooper does not indicate the season of his collection but found all forms from the trout and from the small-mouthed black bass immature. Stafford examined his fresh water fish in the spring and fall. One specimen of his "Megadistomum longum" measured 18. mm. long but contained no eggs; and the largest individuals of his "A. tereticolle" were smaller than immature individuals of Megadistomum. He found that most of his "Mimodistomum angusticaudum" were immature, but "towards the end of October" found a few sexually mature.

Whatever effect the season of collection may have, it is certain that what is evidently the same Azygia species does not attain sexual maturity at the same time in the different hosts in which it occurs. Thus, while average sized forms are producing eggs in such hosts as pike, pickerel, and salmon, specimens fully as large are still immature in such hosts as smelt, trout, small-mouthed black bass, and perch.

That variation in body size at sexual maturity may occur within a single host is shown by Cooper's report of a 14 mm. trematode with less mature eggs than were commonly found in specimens 6 to 14 mm. in length. Further data is needed, however, to show the extent of this variation. It has not been noted by other workers, and certainly is not so conspicuous as the marked differences found in specimens from different hosts.

The maximum body size which the trematode attains also seems associated with the host. In those cases wherein the greatest size is reached (as in the maskinonge and pike) there also seems to be considerable growth before sexual maturity (*e.g.* Stafford's immature 18 mm. specimen), and it is very possible that the ultimate size which the trematode may reach is associated with the amount of growth before eggs are produced, and this latter condition may, in turn, depend upon the fish host.

The following tables (Tables 10–13) show absolute measurements on these different forms. The 66 mm. specimen of *Dist. longum* was very highly extended and had apparently been stretched in killing. Moreover, the body was not equally extended but was more elongate in the uterus region just posterior to the acetabulum. The 37 mm. specimen therefore probably furnishes the more normal proportions.

TABLE 10. *Azygia sebago*

Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
5.9	0.9	0.65	0.59	2.	1.4	0.31	2.12	0.72	0.72
5.9	0.9	0.65	0.59	2.	1.4	0.31	2.12	0.72	0.72
10.	0.93	0.65	0.58	4.37	1.9	0.65	2.75	2.	2.
6.7	1.06	0.65	0.56	2.25	1.5	0.41	2.18	1.31	1.18
11.5	0.75	0.67	0.56	4.06	2.	0.5	3.75	2.3	2.4
13.	0.5	0.74	0.56	5.3	2.5	0.9	3.25	1.9	1.9
9.	1.5	0.68	0.62	2.9	1.8	0.4	2.8	1.12	0.55
12.	1.1	0.8	0.5	4.8	3.	2.12	3.43	1.9	1.9
10.	0.81	0.71	0.52	4.18	2.56	1.3	3.18	1.93	2.28
10.5	0.81	0.65	0.56	3.6	2.4	1.06	3.37	2.12	1.87

TABLE 11. *Azygia bulbosa*

Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
5.68	1.	0.81	0.62	2.43	1.68	0.65	1.49	0.75	0.75
6.3	1.37	0.87	0.62	2.2	1.8	0.65	1.5	0.75	0.75
6.2	1.25	0.81	0.68	2.4	2.1	0.58	1.6	0.7	0.7
8.4	2.9	1.25	1.	2.6	2.5	0.84	2.5	1.32	1.25
3.9	0.9	0.66	0.54	1.25	1.5	0.37	0.78	0.28	0.28
5.6	0.9	0.69	0.54	2.	1.6	0.58	1.6	0.73	0.92
7.1	1.1	0.87	0.63	2.	2.5	0.69	2.1	1.2	1.2
5.1	1.	0.75	0.56	1.68	1.62	0.9	1.3	0.74	0.74
4.18	0.9	0.56	0.35	1.3	1.49	0.5	1.12	0.55	0.55
6.9	1.1	0.81	0.62	1.9	2.	0.8	2.3	1.43	1.43
5.9	1.1	0.75	0.63	1.9	1.8	1.56	1.6	0.85	0.85

TABLE 12. Cooper's *Azygia lucii* from *L. masquinongy*

Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
29.	2.06	1.06	1.06	15.3	4.	4.8	6.87	3.27	4.07
29.	2.1	1.1	1.1	12.3	4.4	7.5	9.6	4.	6.1
39.	2.18	1.25	1.25	17.	4.3	8.2	9.	5.6	4.4
31.	1.8	1.	1.	14.	3.68	5.3	9.1	5.23	3.3
	2.3	1.25	1.37		5.12	9.7			
	1.87						8.4	6.22	5.9
	1.68						9.6	5.3	6.8
		1.18	1.18						
		0.87	0.87						
3.4	0.5	0.48	0.5						

The large size of *Dist. longum* and the form from the maskinonge seems at first to separate them from most of the other forms. Leidy's *Dist. tereticolle,* however, somewhat bridges the gap.

The equal size of the suckers in the form from the maskinonge is distinct in these tables, but Cooper himself reports the oral sucker as larger than the acetabulum. In *Dist. longum* which this form most closely resembles, the oral sucker is larger. Moreover, Ward reports occasional equality of sucker-size in *A. sebago.* In view of these facts, the apparently constant equality of the size of the suckers in the above form is probably a coincidence, and at any rate could not alone justify a new species.

TABLE 13. Cooper's *Azygia lucii* from the pike

Measurements in millimeters

Length	Width	Oral sucker	Acetabulum	Post. edge acet. to mid. ovary	Post. edge acet. to ant. end	Post. edge acet. to most ant. vitellaria	Post. edge testis to end	Vit. on left beyond testis	Vit. on right beyond testis
142	1.6	0.93	0.75	4.18	2.7	0.25	5.	2.8	2.5
14.	1.12	0.78	0.56	6.3	2.9	0.89	5.	2.7	2.3
8.	1.	0.5	0.43	3.75	1.8	0.48	1.75	0.75	0.68
11.	0.75	0.68	0.56	4.75	2.5	1.5	2.68	1.18	1.37
7.5	0.87	0.67	0.52	2.9	1.6	0.28	2.	0.9	0.87
8.5	0.68		0.5	3.4	1.8	0.43	1.4	0.8	0.8
12.	0.93	0.75	0.62	5.5	3.9	0.9	2.18	1.5	1.
Leidy's *Distomum tereticolle*									
20.3	0.97	0.8	0.71	9.3	3.9	2.5	7.1	3.6	3.6
Distomum longum									
66.	1.56	1.42	1.3	38.	6.8	18.7	12.1	7.1	7.1
37.	1.56	1.37	1.18	19.7	5.68		9.	4.	4.

The egg size is larger in the larger forms, but intermediate sizes were found in some of the material from the pike as shown by the following measurements.

TABLE 14

Average egg sizes in American forms of Azygia

Azygia sebago	48 by 27μ
Azygia bulbosa	48 " 28
Leidy's *Distomum tereticolle*	45 " 28
Distomum longum	62 " 34
Cooper's *Azygia lucii* from maskinonge	63 " 33
Cooper's *Azygia lucii* from pike	51 " 28
Cooper's *Azygia lucii* from pike	56 " 28

Two measurements are given in the last case as one trematode from this collection showed larger eggs.

The following tables (Tables 15–18) show the ratios of body length to: (1) width, (2) "neck" region, (3) uterus region, and (4) distance between ventral sucker and most anterior vitellaria.

TABLE 15

PROPORTION OF BODY LENGTH TO WIDTH IN AZYGIA SPECIES
BODY LENGTH IN MILLIMETERS IS GIVEN IN PARENTHESES

A. sebago		*A. bulbosa*		*A. angusticauda*		*A. acuminata*	
6.5	(5.9)	5.68	(5.68)	7.7	(5.25)	3.8	(6.8)
11.7	(10.5)	4.6	(6.3)	7.9	(4.9)	3.6	(6.5)
6.2	(6.7)	5.	(6.2)			4.2	(6.3)
11.8	(10.)	3.	(8.4)			3.7	(7.5)
15.3	(11.5)	4.3	(3.9)			4.7	(8.)
26.	(13.)	6.2	(5.6)			4.5	(11.3)
6.	(9.)	6.5	(7.1)			4.3	(10.9)
10.9	(12.)	5.1				7.5	(9.75)
12.3	(10.)	4.6	(4.1)			3.8	(9.68)
		5.3	(6.9)			6.3	(9.87)
		4.4	(5.9)			7.2	(9.37)
Cooper's *A. lucii* from pike		Cooper's *A. lucii* from maskinonge		*Dist. longum*		Leidy's *Dist. tereticolle*	
8.7	(14.)	14.5	(29.)	42.2	(66.)	20.8	(20.3)
12.	(14.)	14.5	(29.)	23.5	(37.)		
14.6	(11.)	17.8	(39.)				
8.6	(7.5)	6.8	(3.4)				
12.9	(12.)						
8.	(8.)						

TABLE 16

PROPORTION OF THE TOTAL BODY LENGTH TO THE DISTANCE FROM VENTRAL SUCKER TO ANTERIOR END IN AZYGIA SPECIES

Body length in millimeters is given in parentheses

A. sebago		*A. bulbosa*		*A. angusticauda*		*A. acuminata*	
4.2	(5.9)	3.3	(5.6)	2.	(5.25)	2.4	(8.)
5.2	(10.)	3.5	(6.3)	2.	(4.9)	2.9	(11.3)
4.4	(6.7)	3.	(6.2)			2.8	(10.9)
5.7	(11.5)	3.3	(8.4)			3.1	(9.75)
5.2	(13.)	2.6	(3.9)			2.6	(9.68)
5.	(9.)	3.5	(5.6)			2.7	(9.87)
4.	(12.)	3.	(7.1)			2.7	(6.87)
3.9	(10.)	2.7	(4.1)			3.7	(6.56)
4.	(10.5)	3.4	(6.9)			2.8	(6.3)
		3.3	(5.9)			2.7	(7.5)
Cooper's *A. lucii* from pike		Cooper's *A. lucii* from maskinonge		*Dist. longum*		Leidy's *Dist. tereticolle*	
5.2	(14.)	7.2	(29.)	9.7	(66.)	5.2	(20.3)
4.8	(14.)	6.6	(29.)	6.7	(37.)		
4.4	(8.)	9.	(39.)				
4.7	(7.5)	8.3	(31.)				
4.4	(11.)						
4.7	(8.5)						
4.	(12.)						

TABLE 17

PROPORTION OF TOTAL BODY LENGTH TO LENGTH OF UTERUS REGION IN AZYGIA SPECIES

Body length in millimeters is given in parentheses

A. sebago		*A. bulbosa*		*A. angusticauda*		*A. acuminata*	
2.9	(5.9)	1.9	(5.68)	2.8	(5.25)	3.6	(6.87)
2.2	(10.)	2.8	(6.3)	2.9	(4.9)	2.8	(6.56)
2.9	(6.7)	2.5	(6.2)			3.1	(6.3)
2.9	(11.5)	2.5	(8.4)			2.8	(7.5)
2.4	(13.)	2.3	(3.9)			3.	(8.)
3.	(16.)	2.8	(5.6)			3.2	(10.9)
2.5	(12.)	3.5	(7.1)			2.95	(9.75)
2.3	(10.)	3.	(5.1)			3.2	(9.68)
2.6	(10.5)	3.2	(4.18)			2.7	(9.87)
		3.6	(6.9)				
		3.	(5.9)				

Cooper's *A. lucii* from pike		Cooper's *A. lucii* from maskinonge		*Dist. longum*		Leidy's *Dist. tereticolle*	
3.3	(14.)	1.9	(29.)	1.7	(66.)	2.2	(20.3)
2.2	(14.)	2.3	(29.)	1.8	(37.)		
2.1	(8.)	2.3	(39.)				
2.3	(11.)	2.2	(31.)				
2.6	(7.5)						
2.5	(8.5)						
2.2	(12.)						

TABLE 18

PROPORTIONS OF THE BODY LENGTH TO THE DISTANCE FROM VENTRAL SUCKER TO THE MOST ANTERIOR VITELLARIA IN AZYGIA SPECIES

Body length in millimeters is given in parentheses

A. sebago		*A. bulbosa*		*A. angusticauda*		*A. acuminata*	
19.	(5.9)	8.7	(5.68)	26.2	(5.25)	20.	(8.)
14.4	(13.)	9.7	(6.3)	27.2	(4.9)	17.3	(11.3)
16.7	(6.7)	10.6	(6.2)			29.4	(10.9)
22.5	(9.1)	10.	(8.4)			19.5	(9.7)
15.5	(12.)	9.6	(5.6)			28.2	(9.8)
5.6	(19.)	10.5	(3.9)			3.2	(9.68)
23.	(11.5)	10.2	(7.1)			complete	(6.8)
7.5	(10.)	5.7	(5.1)			13.1	(6.56)
9.9	(10.5)	8.3	(4.18)			28.6	(8.87)
		8.6	(6.9)			12.5	(9.37)
		10.5	(5.9)			22.	(11.)
						complete	(6.3)
						complete	(7.5)

Cooper's *A. lucii* from pike		Cooper's *A. lucii* from maskinonge		*Dist. longum*		Leidy's *Dist. tereticolle*	
45.	(14.)	6.	(29.)	3.5	(66.)	8.1	(20.3)
15.7	(14.)	3.8	(29.)				
16.6	(8.)	4.7	(39.)				
7.3	(11.)	5.8	(31.)				
26.7	(7.5)						
19.7	(8.5)						
13.	(12.)						

The relative width of the body is seen to be quite variable. Differences can be explained by different degrees of contraction, and by growth changes. The closely related genus, Otodistomum, has been shown to increase greatly in length but very little in width with growth. This condition is well shown by reference to the 39 mm. and the 3,4 mm. specimens (Table 12) from the maskinonge. In the former case the length is 17.8 times the width while in the latter the length is only 6.8 times the width.

Dist. longum and the form from the maskinonge have body lengths 7 to 9 times the neck regions, while in the other forms this ratio varies from about 3 to 5. But this difference is of no specific significance, being clearly due to the larger size of the former trematodes and representing a change in ratio which has been shown to occur with growth in similar forms. That is, the proportions shown in the table are what would be expected if all the forms represented different stages of growth of the same species. In the 66 mm. specimen of *Dist. longum* some allowance should perhaps be made for artificial extension which the other specimens did not receive.

The tables dealing with the uterus length and with the anterior extent of the vitellaria both indicate a slight tendency in *Dist. longum* to differ from the other species. In regard to uterus length, however, the smallest ratio (1.7) or longest uterus is in the specimen already described as showing a localized extension in that region. Furthermore, a tendency for this region normally to increase slightly its proportion to the remainder of the body was shown to be true in Otodistomum.

The anterior extent of the vitellaria is highly variable, as the body may be from 3.5 to 45 times the length of the distance between vitellaria and the acetabulum. Because of this high variation and because there is no consistency in any single group outside of *A. acuminata*, this point cannot be urged in separating species.

Thus, in spite of the great difference in size, a consideration of the possible features which might separate these species shows that there has been found no valid basis for distinction between them. It is especially significant that, except for characters which vary and overlap in the different forms, all the differences are in the direction taken by normal growth changes, and are moreover commensurable with such changes. Therefore, one feels justified in concluding that so far as can be determined morphologically, all these forms are representatives of the single species, *Azygia longa* (Leidy), and that this species manifests a variety of states, the extremes of which differ widely, but all of which are in accordance with growth changes and capacities known in related trematodes. The following fish are known hosts: *Salmo sebago*, *Osmerus mordax*, *Esox reticulatus*, *Anguilla chryspa*, *Perca flavescens*, *Esox lucius*, *Amiatus calvus*, *Esox masquinongy*, *Salvelinus namaycush*, *Lucioperca* sp., *Micropterus dolomieu*.

AZYGIA ROBUSTA ODHNER 1911

Odhner (1911b) established the species, *A. robusta*, "mit einer gewissen Reserve." This form (from the salmon) differs from *A. lucii* apparently in attaining a somewhat greater length (to 47 mm.) and in possessing a spherical although "mitunter etwas langer als breit" pharynx. The latter feature is the chief one upon which the species is founded. Odhner in his "ziemlich reichlichen Material" never finds the pharynx twice as long as wide, while in the material (*A. lucii*) from the pike, the pharynx is never spherical but always elongate. In a postscript, Odhner claims a substantiation of this new species on the character of the pharynx. As he gives no further specific differences between the new species and *A. lucii* it is to be inferred that the two are similar in other respects.

This distinction on pharynx shape introduces a new possible taxonomic factor for the group. The following measurements from favorable total mounts and cleared specimens might help in estimating the value of this character. The longitudinal axis of the pharynx is the first measurement given in each case. All measurements are in millimeters.

Otodistomum cestoides

0.54×0.39	0.48×0.39	0.37×0.24
0.56×0.37	0.71×0.56	0.35×0.26
0.46×0.41	0.54×0.50†	0.43×0.37
0.18×0.18*	0.50×0.29	0.37×0.37*
0.24×0.16	0.18×0.15	0.35×0.28
0.20×0.18†	0.56×0.39	0.56×0.46
0.18×0.16†	0.24×0.18	0.74×0.56
0.22×0.16	0.52×0.43	0.74×0.74*
0.18×0.15	0.46×0.35	0.44×0.31
0.46×0.37	0.37×0.29	

A. sebago	*A. bulbosa*	*A. acuminata*
0.35×0.20	0.31×0.31*	0.41×0.26
0.28×0.37*	0.20×0.22*	0.37×0.35†
0.18×0.11	0.37×0.41*	0.37×0.31
0.37×0.20	0.29×0.22	0.18×0.18*
0.46×0.28	0.29×0.28†	0.27×0.27*
0.28×0.18	0.41×0.41*	0.31×0.24
0.37×0.28		0.46×0.45†
0.28×0.22		
0.28×0.20		
0.20×0.14		

A. loossii	Cooper's *A. lucii*	*Dist. longum* Leidy
0.18×0.14	0.62×0.37	0.65×0.50
0.18×0.14	0.65×0.43	0.65×0.46
0.18×0.13	0.48×0.29	
	0.37×0.27	
	0.40×0.31	
	0.37×0.34†	
	0.32×0.27	

* indicates that the pharynx is at least as wide as long.
† indicates that the pharynx is practically as wide as long.

A study of these figures shows that in no American species does the pharynx measure twice as long as wide; that it is ovoid rather than cylindrical; and that in all cases it may assume an almost spherical shape. For the European species, *A. lucii*, Looss (1894) describes the pharynx as cylindrical and his figure shows its length to be twice its width. Of this species Odhner (1911b:520) says: "Pharynx immer langgestreckt, etwa doppelt so lang wie breit, bei 18–22 mm. langen Exemplaren 0.6–0.8 mm. lang und 0.35–0.45 mm. breit." Accepting these records, there appears to be rather definite difference between *A. lucii* and all American species in the shape of the pharynx. Odhner's *A. robusta* resembles the American species in this respect. In view of the range of variability shown by the above measurements, this feature becomes of questionable specific value, particularly when considered alone. But until further comparisons with numerous specimens of European forms are made, the conclusions of Odhner will be accepted.

AZYGIA PERRYII FUJITA 1918

Fujita (1918) described this species from a fresh-water fish, *Hucho perryi* Breevoort, sent him by a friend. Fujita found the trematode attached to the external surface of the fish especially to the pectoral fin, oral cavity, buccal cavity, and outer and inner surfaces of the operculum and gills. This location of the parasite, although emphasized by Fujita, is, of course, of no significance since Azygia species normally inhabiting the anterior regions of the digestive system often migrate forward into the oral cavity and hence to the exterior. Such migration was noted as conspicuous in *A. sebago* by Ward (1910).

Fujita compares a few relative measurements of his form with *A. lucii* and *A. sebago*. His table of comparison follows. The figures are in percentages presumably based upon body length.

	A. perryii	Average	A. sebago	Average	*A. lucii*
Distance between oral and ventral suckers	18 19 17 18 18	18%	16 22 24 11 19	18%	24
Distance from anterior tip to center of ovary	54 53 47 50 49	51%*	54 56 54 63 66	59%	63
Center of ovary to center of post. testis	62 59 59 57 58	59%*	65 65 66 77 74	69%	74
Breadth behind ventral sucker	14 14 14 12 15	14%	16 21 17 6 19	16%	8

* These two numbers are interchanged in the original table, but it is obvious that this is due to misprinting.

Fujita concludes from these figures that his species "has a resemblance to the American species in the distance between suckers and breadth of body, but in the location of the reproductive organs, which is very important, it is entirely different from the American species. On the other hand, the European species resembles closely the American species in positon of reproductive organs, and on other points it differs from both American and Japanese forms." He does point out that these percentages are of comparative value only, since they will vary according to the methods used in preserving the specimens.

But Fujita's conclusions from his table are open to still more serious objections. The number of specimens compared is small as measurements of the single case of *A. lucii* were calculated from the figure by Looss (1894). Furthermore, all of the characters considered are influenced by different degrees of contraction and a contraction of any particular region of the body would alter such percentages. This fact might account for the high variation in the figures for *A. sebago.* But still more important, an analysis of the figures as they stand shows no valid differences between the three forms. The figures for *A. sebago* cover a range which includes figures for both the other forms in every character considered except "center of ovary to center of posterior testis" where 62% in *A. perryii* is the nearest approach to 65% in *A. sebago.* It is quite unexplained how "the position of the reproductive organs" in *A. perryii* is "entirely different" from the other two species. The derivation of the percentages in the character dealing with this distance from the ovary to the posterior testis is also not clear. The percentages (62% to 74%) certainly cannot be in relation to body length as the other figures appear to be, and 6.2% to 7.4% likewise are inappropriate for such ratio.

Two type specimens of *A. perryii* in the Ward Collection* were available for study. Measurements of these specimens are as follows:

Length	8.6 mm.	5.6 mm.
Width	1.3	0.8
Oral sucker	0.78	0.58
Acetabulum	0.6	0.48
Post. edge acetab. to mid. ovary	2.	1.06
Post. edge acetab. to anterior end	2.18	1.8
Post. edge acetab. to most ant. vitellaria	right: 0.18 left: 0.56	0.09
Post. edge testis to post. end	3.1	1.9
Vit. on left beyond testis	0.74	0.84
Vit. on right beyond testis	0.2	*1.3
Pharynx	0.317 x 0.28	0.24 x 0.11

Fujita figures the vitellaria as terminating posteriorly in the immediate neighborhood of the posterior testis. I found that the posterior extent of the vitellaria was only slightly beyond the testis in the 8.6 mm. specimen, although they extended slightly over 1/2 the distance between this point and the posterior end on one side only in the 5.6 mm. specimen. In respect to this important point, Fujita says: "The posterior extent (of the vitellaria) extends somewhat farther down than the posterior testis" and adds that the vitellaria "do not extend posteriorly as far as in the American form." Since it has been seen that the vitellaria in *A. lucii* may extend some distance beyond the hind testis, it is apparent that *A. perryii* is like *A. lucii* and different from the American species in this respect.

Concerning the anterior extent of the vitellaria, Fujita says they reach "to near the posterior end of the ventral sucker," and concludes that this limit is further anterior than is reached by the European species. Looss describes them (in *A. lucii*) as failing to reach the acetabulum by a distance about equal to its diameter (his figure shows them ending posterior to such a point), and this is about their anterior extent as figured by van Beneden (1858). Although in the Japanese material they reach somewhat nearer

* Collection of Dr. H. B. Ward, vial No. 18.83.

the acetabulum, the slight difference in this extent could not separate Fujita's form from the European.

Pharynx measurements of the two specimens in the above table showed one elongate pharynx and one ovoid. Fujita gives 0.29 by 0.2 mm.

Fujita's egg measurement was 0.058 by 0.033 mm. which is larger than the egg size in *A. sebago*, but about the size attained in the American form from the pike. Looss gives 0.045 by 0.023 mm. for *A. lucii*. Hence, in egg size the Japanese appears to differ from the European form, but that this distinction may not be a valid one has been indicated in the preceding comparison of American forms.

Fujita records the presence of the internal longitudinal muscles as described by Ward. He noted also that these muscles were located much more deeply (i.e., farther from the surface) on the dorsal side than on the ventral side. Thus, dorsally the cortical body region measured 0.21 mm., while on the ventral side this same region measured only 0.13 mm. in thickness. Such a condition was not true in American forms I studied. Leuckart's diagram of a cross-section of *A. lucii* is like *A. sebago* in respect to position of these muscles. Some variation in their position is probably accidental.

AZYGIA VOLGENSIS (V. LINSTOW) ODHNER 1911

Synonyms: *Ptychogonimus volgensis* v. Linstow 1907
Distomum volgense (v. Linstow) Lühe 1909

Odhner states that this species (from *Lucioperca sandra*) appears to be a true form. Apparently only very few specimens are known, v. Linstow studying only one. "Lühe's (1909) description is based on von Linstow's. Odhner (1911b) does not state the number or source of specimens he studied. His description is, however, very brief." It is certainly very close to *A. lucii* and no important distinction can be determined between the two from their descriptions. The length of *A. volgensis* is 5 mm. according to Odhner, and 6.2 mm. according to v. Linstow. Odhner contrasts "Eiproduktion" in *A. volgensis* at 2 mm. with this condition at 5 to 6 mm. in *A. lucii*, an entirely meaningless feature, in view of the variation the condition shows in American forms. These two European species should be further studied. On the basis of present evidence *A. volgensis* must be regarded as a doubtful species.

SYNOPSIS OF THE GENUS AZYGIA

A key to the species of Azygia (including the several doubtful European species which might represent the single form, *A. lucii*) follows:

Vitellaria not extending appreciably posterior to the hind testis
- Body length about 6 mm.; sexually mature at 2 mm. . . . . *A. volgensis* (v. Linst.)
- Body length up to 30 mm. or more
  - Pharynx elongate, twice as long as wide; eggs 45 by 23μ. . . . . *A. lucii* (Muell.)
  - Pharynx globose; eggs? . . . . *A. robusta* Odhner
    - Eggs 58 by 33μ. . . . . *A. perryii* Fujita

Vitellaria extending considerably posterior to the hind testis, usually at least half way between this point and posterior end of body
- Acetabulum near middle of body; gonads near posterior tip. . *A. angusticauda* (Staff.)
- Acetabulum distinctly nearer the anterior end; gonads anterior from posterior tip by about 1/3 ot 1/4 the body length
  - Body relatively wide; vitellaria beginning close behind acetabulum; neck usually constricted; internal parenchyma muscles weak; eggs about 64 by 33μ. . . . . *A. acuminata* Goldberger
  - Body often extremely elongate; vitellaria usually beginning some distance posterior to acetabulum; internal parenchyma muscles strongly developed; eggs variable in size (up to 63μ in length), usually about 48 to 55μ by 28 to 30μ. . . . . *A. longa* (Leidy)

A GENERAL STUDY OF SOME MARINE FISH TREMATODES

Most of the following trematodes were collected at the Mount Desert Island Biological Laboratory during the summer of 1924. A brief account of these parasites has already been published (Manter 1925). The following descriptions give more complete data on them. A few trematodes from fish of the Woods Hole region are also considered. The study of these forms is based on specimens from the collection of Dr. Henry B. Ward. Extended descriptions are given only to those forms which are new or which have been briefly or incompletely described in the literature. Following the systematic arrangement adopted by Nicoll (1915) for trematodes of British fish, the forms studied would be grouped as follows:

Order: DIGENEA
Sub-order: Prostomata
Super-family: Distomata
Family: Allocreadiidae
Sub-family: Allocreadiinae
Genus: Podocotyle
1. *P. atomon*
2. *P. olssoni*
Sub-family: Stephanochasminae
Genus: Stephanochasmus
1. *S. baccatus*
Sub-family: Lepocreadiinae
Genus: Lepidapedon
1. *L. rachion*
2. *L. elongatum*
Genus: Homalometron
1. *H. pallidum*
Family: Zoogonidae
Sub-family: Lecithostaphylinae
Genus: Steganoderma
1. *S. formosum*
Family: Siphoderidae*
Genus: Siphodera
1. *S. vinaledwardsii*
Family: Azygiidae
Genus: Otodistomum
1. *O. cestoides*
Family: Hemiuridae
Sub family: Hemiurinae
Genus: Hemiurus
1. *H. levinseni*

* Odhner may be correct in not recognizing this family.

Sub-family: Sterrhurinae
Genus: Brachyphallus
1. *B. crenatus*
Sub-family: Lecithasterinae
Genus: Lecithaster
1. *L. gibbosus*
Genus: Aponurus
1. *A. sphaerolecithus*
Sub-family: Syncoeliinae
Genus: Derogenes
1. *D. varicus*
Genus: Genolinea
1. *G. laticauda*
Genus: Gonocerca
1. *G. phycidis*
Sub-family: Accacoeliinae
Genus: Hirudinella
1. *H. fusca*
Unclassified genus: Deropristis
1. *D. inflata*
Order: MONOGENEA
Family: Tristomidae
Sub-family: Acanthocotylinae
Genus: Acanthocotyle
1. *A. verrilli*
Family: Octocotylidae
Sub-family: Octocotylinae
Genus: Dactycotyle
1. *D. minor*

THE GENUS PODOCOTYLE

Stafford (1904) records "*Sinistroporus simplex* Rud." from seven different Canadian marine fish. He comments: ". . . . genital pore to the left from the origin of the caeca in all specimens examined," and on this basis seems to found the new genus, Sinistroporus. The species is evidently the *Dist. simplex* Rud. that Linton describes from various fish of the Woods Hole region. The sinistral position of the genital pore is not sufficient, however, to separate the form from the genus Allocreadium in its older sense. Odhner (1905) considers *Dist. simplex* Rud. as probably synonymous with *Podocotyle atomon* (Rud.) and he also includes *Dist. simplex* Rud. of Levinsen (1881) as a synonym. Odhner redescribes the genus Podocotyle with *Dist. atomon* Rud. as type.

Podocotyle, originally a sub-genus of Dujardin's, was listed as a genus by Stossich in 1892. Stiles and Hassall (1898) established as type of this genus *Dist. angulatum* Duj. This species is, however, a species inquirenda, and Lühe (1900:491) remarks: Das endgültige Schichsal der Gattung ist demnach abhängig davon, dass diese Spec. inquir. einmal wieder gefunden

und dann auch wieder erkannt wird." According to Odhner (1905:321) this type material has been permanently lost, and the species is insufficiently described. He therefore assign: *Dist. atomon* Rud. as type species of Podocotyle. At any rate, the forms described as Sinistroporus are without doubt members of this genus as separated from Allocreadium. Such a synonymy is recognized by Nicoll in 1909 when he lists Sinistroporus Staff. as synonymous with Podocotyle (Duj.) Odhner. In an earlier paper Odhner (1901) had considered *Allocreadium atomon* (Rud.) as a highly variable species and recognized three varieties. In 1905, he determines *Podocotyle atomon* (Rud.) (=*Allocreadium atomon* (Rud.) Odhner 1901, e.p.) as a fixed species and his earlier varieties he considers as true species.

The diagnosis of the genus Podocotyle as given by Odhner (1905) is as follows: "Body elongate, quite evenly wide, sometimes flattened and ribbon-like, sometimes cylindrical. Esophagus at most twice as long as pharynx, forking in front of the ventral sucker. Genital pore to the left, lying at the level of the esophagus. Excretory vesicle reaching to the ovary. Cirrus-sac elongate, reaching at maximum as far as half way between ventral sucker and ovary. Seminal vesicle long, coiled. Pars prostatica lacking. Cirrus of marked length, straight. Ovary three-lobed. Vitellaria normally not reaching anterior to ventral sucker. Eggs without filament. In intestine of marine fish. Type species *P. atomon* (Rud.) Other species, *P. reflexa* (Crep.), *P. olssoni* Odhner (=*Dist. simplex* Olss. 1868 e.p.)."

Odhner refers to Linton's form as either identical with *P. olssoni* or closely related to it. Two species of Podocotyle were found in the present collection and these tend to confirm the constancy of the specific nature of the characters given by Odhner. In *P. atomon* the vitellaria are unbroken and do not come together between the testes; the testes are relatively small, not occupying over one half the cross-section of the body; the esophagus is longer than the pharynx; and the cirrus sac over-reaches the ventral sucker by a short distance. In both *P. reflexa* and *P. olssoni*, the vitellaria are broken near each testis and come together between these organs; and in both species also the testes are large, occupying a great part of the body in cross-section. *P. reflexa* differs in being cylindrical. It also has an esophagus longer than the pharynx. *P. olssoni* possesses and esophagus only as long or even shorter than the pharynx; and has a seminal vesicle reaching about half way between ventral sucker and ovary.

PODOCOTYLE ATOMON (RUDOLPHI 1802)
[Fig. 49]

From intestine, *Pholis gunnellus* (Butterfish)
From intestine, *Anarrhichas lupus* (Wolf fish)

One specimen of this species was taken from each of two butterfish of ten examined. These trematodes measured 2.37 mm. and 2 mm. in length.

Both of the specimens agreed in detail with Odhner's description of the species, with long esophagus, small testes, and unbroken vitellaria (Fig. 49). In one specimen the body was somewhat contracted and in this case the esophagus coiled somewhat instead of shortening with contraction, so that its length could be easily distinguished as about twice that of the pharynx Cooper (1915) reports one young specimen of *Sinistroporus simplex* from the butterfish, but it is very probable that he was dealing with the same species now being considered. Both of the present specimens were fully mature.

The single specimen from the wolf-fish measured 3.06 mm. in length and 0.57 mm. in width. The esophagus was twice the pharynx length. The testes occupied about half the body width and were slightly lobed or crenulated as Cooper noted for *Sinistroporus simplex.* There was a slight break in the vitellaria opposite the hind testis, and the follicles approached each other between the testes. In these respects, the form showed a tendency to assume characters of *P. olssoni*, although these features are more marked in the latter species. In view of this possible variation of the vitellaria, the esophagus length seems to be the most useful distinction between the species.

PODOCOTYLE OLSSONI ODHNER 1905
[Fig. 50]

From intestine, *Urophycis tenuis* (Hake)
" " *Myxocephalus groenlandicus* (?) (Sculpin)
" " *Gadus callarias* (Cod)
" " *Microgadus tomcod** (Tomcod) Woods Hole

This trematode is a very common species. Fig. 50 shows the typical appearance of the material from the hake. The differences between this species and *P. atomon* have already been pointed out. The specimens from the hake show these differences most constantly and clearly. The esophagus is short (not longer than the pharynx); the seminal vesicle reaches to a point about half way between ventral sucker and ovary; the testes are large; and the rows of vitellaria are broken opposite each testis. The size was from 2.8 to 4 mm. in length by 0.4 to 0.58 mm. in width. The ventral sucker is prominent, usually somewhat protruded, and longer in its cross-diameter. It is almost exactly twice the size of the oral sucker. In one specimen the body wall about the sucker formed a slightly projecting fold around the sucker.

Material from the cod (which were of small size) agrees with the Woods Hole material from the tomcod. These forms show a few slight differences from the clear-cut specific characters of the form from the hake. The short

* Collection of Dr. H. B. Ward, vial No. 13.75.

esophagus, however, is a constant character in which all agree.The breaks in the rows of vitellaria can usually, but not always, be discerned in the cod trematodes. The one or two cases wherein the follicles appeared continuous were of somewhat contracted specimens. The forms from the cod were all small in size. They measured 1.28 to 1.6 mm. by 0.26 to 0.3 mm. The seminal vesicle did not quite reach to a point half way between ventral sucker and ovary.

All of these forms also show two regions of slight body contraction, one about at the level of the posterior testis, the other usually slightly in front of the anterior testis. Figure 50 shows this condition only slightly evident. Sometimes it is conspicuous. Odhner does not mention it, nor does Linton, although the condition is shown in the figure of his *Dist. simplex* from the tomcod (Linton 1898, pl. 47, fig. 3). From Linton's description and figures there can be no doubt that his *Dist. simplex* (Linton 1898:525) is the same species as the present form from the tomcod. Linton records a length up to 2.4 mm., which approaches the size of the material from the hake. The egg size in all forms agrees, being 70 to 80 by 37 to 40μ. Considering the above characteristic features, there can be little doubt that all the forms belong to the species, *P. olssoni.*

STEPHANOCHASMUS BACCATUS NICOLL 1907

[Figs. 51–52]

From intestine, *Hippoglossus hippoglossus* (Halibut)

Five specimens of this trematode were obtained from the intestine of a single halibut. The largest specimen containing about 12 eggs measured 2.18 mm. in length. The smallest containing one imperfect egg was about 1.3 mm. in length. Measurements on the large specimen are as follows:

Length	2.187 mm.
Width	0.467
Oral sucker	0.176
Ventral sucker	0.256
Pre-pharynx	0.2
Pharynx	0.199 by 0.119
Eggs	85 to 91 by 45 to 51μ
Length of spines in posterior row	34μ
Length of spines in anterior row	28μ

In two specimens the number of spines in the oral ring was 29, but that this number may vary is shown by the fact that only about 25 spines were found in a third specimen. Nicoll found from 28 to 30 spines. The ring is unbroken, and the spines in the posterior ring are larger than those in the anterior ring.

The characteristic shape of the egg with one pole flattened was noted (Fig. 52). This condition at first seemed due to contraction, but Nicoll

reports it as specifically characteristic. In cross-section the eggs show a peculiar star-shaped outline (Fig. 52), which is evidently characteristic for all species in the genus.

LEPIDAPEDON RACHION (COBBOLD) STAFFORD 1904
[Figs. 45–46]

Syn.: *Lepodora rachiaea* (Cobbold) Odhner 1905
From intestine, *Melanogrammus aeglifinus* (Haddock)

This trematode is fairly common and well known. Nicoll and Lebour each report it as common in the haddock of the English coast. Infection, however, is always light, usually only from one to three trematodes being found in a host. Its presence might accordingly be easily overlooked. In the present collection, two specimens were found from one host, and one each from two others. It is reported by Stafford (1904) from the same host. Stafford gives it the new generic name, Lepidapedon (for the form previously known as *Dist. rachion* Cobbold), but gives no description. Odhner (1905) gives a complete and carefully worked out description of the form which he named *Lepodora rachiaea* (Cobbold). In spite of the extent of Odhner's work, Stafford's name, Lepidapedon, holds priority and has been accepted by Nicoll and others. Stafford gives the measurement of 5 by 1 mm., but my specimens agree more nearly with those of Odhner who gives a length of 1.5 to 3.5 mm. with a width varying from 1/5 to 1/4 this measurement. The following measurements show general proportions:

Length	2.59 mm.
Width	0.46
Oral sucker	0.24
Ventral sucker	0.18
Pre-pharynx	0.285
Pharynx	0.19 by 0.17
X-diameter, ovary	0.11
X-diameter, ant. testis	0.17
X-diameter, post. testis	0.17
Length, sem. ves.	0.285
Cirrus sac	159 by 114μ
Eggs	65 by 34μ

The morphology of the species is well known and the present material showed no new features. Most characteristic is the glandular mass of cells surrounding the seminal vesicle, and the location of the vitellaria ventral to the intestinal ceca.

Two other species of this genus have been described. Leiper and Atkinson (1915) describe a trematode which they name *Lepodora garrardi*. The corrected name would be *Lepidapedon garrardi* (Leip. and Atkin.). The description is not complete in regard to some points and indicates

(as the figure also shows) that their form approaches the genus Lepocreadium which it resembles in body shape and shortened pre-pharynx. No mention is made of any glandular cells surrounding the seminal vesicle.

Odhner mentions one other species but does not describe it. Miss Lebour in 1908 names a species *Lepodora elongata* (= *Lepidapedon elongatum* (Lebour)), and this species she suggests might be the form mentioned by Odhner. It differs from *L. rachion* by being more elongate in form, possessing a long esophagus, and with somewhat less extensive vitellaria. Several specimens, agreeing in most of these points are found in the present collection and were referred to this species.

LEPIDAPEDON ELONGATUM (LEBOUR 1908)
[Figs. 47–48]

Syn.: *Lepodora elongata* Lebour 1908
From intestine, *Urophycis tenuis* (Hake)

Five specimens were collected from one out of three fish examined. The trematode shows close resemblance to *L. rachion* in general form, shape, arrangement of organs, and spiny cuticula, but differs from it in the length of the esophagus, extent and position of the vitellaria, and development of the glandular cells about the seminal vesicle. Also, the genital pore in this species is closer to the ventral sucker than in *L. rachion*. These same differences separate Miss Lebour's *Lepodora elongata* from *L. rachion*. The present form differs only in not being more elongate than *L. rachion*, but this point is one which may be influenced by age of the parasite or by body contraction. Typical measurements are as follows:

Length	2.4 mm.
Width	0.54
Oral sucker	0.119
Ventral sucker	0.14
Pre-pharynx	0.125
Pharynx	0.09
Esophagus	0.091
X-diameter, ovary	0.29
X-diameter, ant. testis	0.31
X-diameter, post. testis	0.37

Miss Lebour does not record the position of the vitellaria in relation to the ceca. As has been noted, in *L. rachion* the vitellaria are ventral to the ceca. In the present form, this condition did not hold but the vitellaria were found distributed on both sides of the intestine. They extend anteriorly at least to the ventral sucker in *L. rachion*, but fail to reach the level of this sucker in *L. elongatum*. Another conspicuous difference between the two species is found in the character of the glandular mass surrounding the seminal vesicle. The cells in this mass are large, globular,

and numerous in *L. rachion* (Fig. 46), but are much reduced in *L. elongatum* where they are very inconspicuous (Fig. 47). In this respect, *L. elongatum* approaches the related genus Lepocreadium. My material also resembles Miss Lebour's and differs from *L. rachion* in that the testes are separated from each other by a distinct space. The pharynx is considerably smaller than in *L. rachion.*

HOMALOMETRON PALLIDUM STAFFORD 1904

[Figs. 54–56]

From intestine, *Fundulus heteroclitus*

This species is the same form referred to by Linton (1901:422, pl. 32, Fig. 354) and named *Homalometron pallidum* by Stafford in 1904. Stafford does not describe the genus or species, merely referring to Linton's paper. Linton's description is as follows:

"Body very minutely spinose, white translucent; acetabulum and oral sucker about the same size; outline of body, long oval; neck short, continuous with body; greatest breadth in region of testes, near posterior end; ecaudate; acetabulum sessile; rami of intestines simple, elongate; esophagus as long as pharynx; testes two, in median line behind uterus; seminal vesicle dorsal to ovary and posterior border of acetabulum; ovary between acetabulum and testes, on right side; pharynx sub-globular; genital aperture in front of acetabulum, on median line; vitelline glands lying at posterior end and along sides of body as far as acetabulum; ova, few, relatively large. Dimensions of specimen in formalin, given in millimeters: Length 2.72; breadth, anterior 0.43, at acetabulum 0.89; middle 1.07, near posterior end 0.36; diameter of oral sucker 0.26; diameter of acetabulum 0.29; diameter of ovary 0.21; diameter of testes 0.33 and 0.39; ova 0.11 and 0.07 in the two principle diameters."

Looss (1907:613–14) criticizes Stafford for establishing a genus without description. As Looss shows, the trematode seems to agree with the genus Lepocreadium Stoss. This genus was established in 1903, or prior to Stafford's Homalometron.

The genus Lepocreadium contains the following species: *L. album* (Stoss.), *L. pegorchis* (Stoss.), *L. trulla* (Lint.) and *L. levinseni* (Lint.). Odhner (1905) erects a new sub-family of the Allocreadiidae, Lepocreadiinae, for this genus and Lepidapedon (=Lepodora). In a later paper (1914) Odhner identifies the cercaria of *Lepocreadium album*, the type species, and gives an account of the morphology of the adult. As is common, some of the most distinctive characters of the genus are found in the distal male genital apparatus.

The present form is strikingly like the genus Lepocreadium. It shows similar size, form, spiny cuticula, suckers, digestive system, excretory

system, vitellaria, and position of the gonads. So far as the description of Linton shows, the form could easily belong to this genus, the chief point of difference being the median location of the genital pore instead of a position to the left, as in Lepocreadium. This pore was clearly median also in my material.

The most important features were found in the male reproductive apparatus. In Lepocreadium a prominent cirrus sac is present. It encloses the prostate gland and an anterior region of the seminal vesicle, which is thus divided into two parts. In the form from Fundulus, however, the cirrus sac is entirely absent. The seminal vesicle is globular and swollen in form and is not divided into two regions (Fig. 55). It opens directly into the pars prostatica, the glandular cells of which lie free in the parenchyma at about the level of the ventral sucker. The prostate gland is poorly developed. The vagina seems to join the male duct shortly beyond the prostate gland and there is a long genital sinus. The absence of a cirrus sac would seem to be of generic significance and, in fact, together with the median genital pore, violates the sub-family diagnosis. Other features of the trematode are so similar to Lepocreadium that it must be considered a very closely related genus.

The seminal receptacle is large and located close behind the seminal vesicle, as in Lepocreadium. A short Laurer's canal is present. No spines could be detected in the cirrus or vagina. The yolk reservoir is large and located posterior to the ovary. The eggs are very large. A specimen with only two eggs showed them to be fully as large or even larger than the ovary. The spiny or scaly cuticula layer is very evanescent as has been noted for Lepocreadium, and may be lost in preserved material. It is most conspicuous on the dorsal anterior regions and thins out in the tail region. The glandular mass about the posterior tip of the excretory vesicle is present as in Lepocreadium.

Very young forms of this distome were sometimes found in large numbers embedded in the intestinal folds of the host. Moreover, from the stomach of the fish cysts were found which clearly contained this trematode as shown by the finely spined cuticula of the cercariae within the cysts. As the Fundulus had been in salt water aquaria for some time, the indication is that infection is derived from marine rather than from fresh water sources. In spite of the fact that immature specimens were sometimes found in large numbers, infection with the adult form was never heavy, and many uninfected fish were found. Usually not more than two or three specimens were taken from one host.

STEGANODERMA FORMOSUM STAFFORD 1904
[Figs. 58–60]

From pyloric ceca, *Hippoglossus hippoglossus* (Halibut)

Six specimens of this interesting trematode were obtained from the ceca of a single halibut. The only description of the form seems to be by Stafford who also found it in the ceca and intestine of the halibut.

The taxonomic position of this trematode is very close to the genus Lecithostaphylus Odhner 1911 (Odhner 1911a) which it markedly resembles, but from which it differs in certain distinct characters. The genus Lecithostaphylus is placed by Odhner in the family Zoogonidae, and, indeed, is used as a basis for a new sub-family, Lecithostaphylinae. Including the present genus, the family contains the following genera:

Family: Zoogonidae
- Sub-family: Lecithostaphylinae
  - Genus: Lecithostaphylus
    - Steganoderma
    - Proctophantastes
    - Lepidophyllum
- Sub-family: Zoogoninae
  - Genus: Diphterostomum
    - Zoogonoides
    - Zoonogenus
    - Zoogonus

Odhner places Lecithostaphylus "an die Spitze der Familie" and from this genus assumes that the entire family might be derived from the, Fellodistominae (Steringophorinae of Odhner*) with which it agrees in genital and digestive systems. In the Fellodistomidae, the cirrus is short and wide, a condition occurring also in Lecithostaphylus but differing from its elongate form in the remaining genera of the Zoogonidae. Steganoderma combines the elongate cirrus with marked similarities to Lecithostaphylus, and hence represents a step between the latter and other genera of the sub-family.

An outline of the genus based on Stafford's description with some additions might be as follows: Body elongate, regular in outline, flattened, both ends regularly rounded, anterior end slightly broader. Scale-like spines covering body to near the posterior end. Suckers about equal in size, ventral sucker a little more than 1/3 from the anterior end. Very small pharynx, long esophagus, ceca extending slightly more than half the body length. Ovary median or to one side, just posterior to the ventral sucker. Testes side by side at ends of ceca. Uterus between testes and filling posterior body. Cirrus sac somewhat elongate, almost straight,

* Nicoll (1913) is correct in pointing out that Odhner is not justified in changing Fellodistominae Nicoll to Steringophorinae.

reaching posteriorly to and sometimes overlapping the ventral sucker, crossing left cecum between ventral sucker and the forking of the intestine. Genital opening ventral and to the left about half way between cecum and margin of body. Vitellaria lateral, reaching only from ventral sucker to the testes, composed of a few large follicles. Laurer's canal present. Type species: *S. formosum* Stafford.

This genus is like Lecithostaphylus Odhn. in body shape, size, spiny cuticula, intestine, gonads, vitellaria, and uterus; but differs from it in possessing a very small pharynx, long esophagus, elongate cirrus, well developed excretory bladder, and Laurer's canal with pore.

The following measurements are from an average sized specimen:

Length	3.25 mm.
Width	0.86
Thickness	0.2 to 0.28
Oral sucker	0.224
Ventral sucker	0.24
Diameter of ovary	0.26
Diameter of testes	0.355
Pharynx	97 by 68μ
Esophagus	0.285
Eggs	34 by 17μ

There is no pre-pharynx. The posterior end of the esophagus splits into two short branches each about 46μ long. That is, the intestine proper does not begin at the point of bifurcation, but the esophagus histologically extends slightly beyond this point.

The excretory system is simple, expanded tube-like in form, and extends from the posterior tip almost to the posterior border of the ventral sucker where it spreads out laterally, T-like. It lies mostly dorsal to the uterus. Near its anterior end it becomes so swollen as to fill the larger part of a cross-section of the body in that region. It here comes in close contact with the intestinal ceca from which it is separated by a very narrow distance (Fig. 59). An excretory duct at the posterior tip of the vesicle is lined by a cuticula-like layer continuous with the external body cuticula. In the parenchyma about this duct appear what seem to be gland cells, pyriform in shape and with large nuclei (Fig. 60).

Within the parenchyma, in the anterior body region, especially in the vicinity of the esophagus, numerous, conspicuous, round to oval bodies occur. They are without nuclei and their content is very finely granular and homogeneous. They exhibit a very strong affinity for eosin stain, which colors them immediately and tenaciously. These bodies which almost fill the parenchyma anteriorly thin out posteriorly, and disappear at about the level of the ventral sucker. Their size varies, being about 13 to 39μ in longest diameter. The nature and function of these bodies could not be determined. They were not found in any other trematode

of the present collection. The cells in the neck region of Siphodera described by Linton (1911) differ markedly from these bodies in appearance. In Siphodera, the cells have definite nuclei.

The position of the ovary is just posterior to the ventral sucker, but it may be either median or slightly to one side. The ootype is small, without membrane, and lies posterior to the ovary. Laurer's canal is present, is only slightly coiled, and opens dorsally just posterior to the ovary. A seminal receptacle seems to be absent. The uterus leads posteriorly, coiling between the testes, filling the hind body, and returning to course ventrally over the ovary. The vagina begins at about the level of the ventral sucker, leads anteriorly and obliquely to the left parallel with the cirrus sac, to which it is at first lateral on the left and then dorsal. The male duct joins the vagina ventrally and there is a common genital sinus for a short distance about 60μ.

The number of follicles in the vitellaria is fairly but not exactly constant. It is sometimes difficult to determine the exact number, as some follicles are seen to be double in nature, an indication of an evolutionary change either toward a more compact or a more diffuse condition of these organs. Eight or nine follicles were found on the right side and ten to twelve on the left.

The two ducts from the testes arise from the anterior aspects of these organs and course anteriorly lateral to the excretory vesicle and between this organ and the ceca. The ducts unite just posterior to the termination of the excretory vesicle, and continue forward for some distance as a single duct in the mid-body region. At about the level of the anterior border of the ventral sucker this duct enters the muscular cirrus sac and becomes the seminal vesicle. This vesicle is poorly developed. It is scarcely, if any, coiled. A slight constriction separates it from the well-developed pars prostatica which, surrounded by gland cells, occupies most of the cirrus sac. The ejaculatory duct is unarmed. In the 3.25 mm. specimen the cirrus sac measured about 0.69 mm. in length and 0.19 mm. in width at its widest point. The seminal vesicle extended about 0.176 mm., the pars prostatica 0.34 mm., and the ejaculatory duct 0.17 mm.

THE HEMIURIDAE

The Hemiuridae include many of the most common marine trematodes. Typical members of the family are those forms with a "tail appendage" such as Hemiurus, Brachyphallus, and Dinurus. Lühe founded the family in 1901, and included in it also such forms as Derogenes and Accacoelium. Looss (1907a) later limited the conception of the family, excluding the two latter genera. Odhner (1911b) points out that Derogenes is so closely related to the other Hemiuridae that separation from that family is impossible. The inclusion of Derogenes necessitates the adoption of

Genarches and other Syncoeliinae. Odhner also included the Accacoeliinae and the *Hirudinella clavata* group. Nicoll reviews the status of the family and agrees with Odhner in accepting its broader conception according to which "Looss's Hemiuridae takes the position of a sub-family" (Nicoll 1913:245). Nicoll also extends the boundaries of the family slightly to include his genera, Hemipera and Derogenoides. The family has thus become so broad as to be very difficult to describe. At present, it must be considered as a large variable group, containing (Nicoll 1915) the following sub-families: Hemiurinae, Diurinae, Sterrhurinae, Lecithasterinae, Syncoeliinae, and Accacoeliinae. Considering Hirudinella as belonging in the last sub-family, members of each of these sub-families except Dinurinae have been met with in the present studies.

A few words should be said in respect to the use of the term "cirrus sac" in this group (Hemiuridae). In the Hemiuridae, the two sex ducts unite to form a more or less elongate tube-like "ductus hermaphroditus" or genital sinus which leads to the common genital pore. This condition of the terminal genital region in the Hemiruidae has been rather fully discussed in the literature. Pratt (1898) reviews the situation and gives its history to 1898. Levinsen (1881) and Juel (1889) termed the common terminal portion of the genital tract the genital vestibule. It is perhaps now more commonly known as the genital sinus. Pratt and Juel both believe that the terminal portion of this vestibule or genital sinus has arisen as "an invagination of the body wall and is homologous to the genital cloaca of other trematodes." Juel believes that the remainder of the duct represents the distal end of the uterus which has come to serve as a genital sinus by the dropping back of the ejaculatory duct. Pratt, however, believes that it has been the uterus that has dropped back and hence that most of the sinus is homologous with the forward end of the ejaculatory duct.

Whatever its origin, it is known that this genital sinus can function as a cirrus, and is protrusible. Looss noted such a functioning in 1896 for *Apoblema mollissimum.* Because the genital sinus functioned as a true cirrus, the muscular sac surrounding it he considered as a true cirrus sac. He says (p. 125): "Or, en ne tenant compte que de ses rapports avec le canal renfermé, je crois déjà pouvoir la considérer avec raison comme une véritable poche du cirrhe: ces fonctions viennent parfaitment à l'appui de cette interprétation." In the same discussion, however, Looss himself notes that the term is not strictly correct. Thus, in regard to "la poche du cirrhe," he says (p. 127): . . . . "à proprement parler ce terme n'est pas tout à fait exact; mais connaissant maintenant ses rapports avec le reste des organes génitaux, nous pouvons nous en servir pour plus de simplicité." Other authors (e.g., Lühe 1901, Lander 1904, Odhner 1905,

Lebour 1908) agree in calling the muscular sac around the genital sinus a true cirrus sac.

Strictly speaking, it does not seem appropriate to refer to this structure as a true cirrus sac. The cirrus is a definite organ belonging strictly to the male genital system. The genital sinus in Hemiuridae, although functioning as a cirrus and although probably homologous with the cirrus, cannot be termed a true cirrus, since it is a duct common to both male and female systems. It has never been referred to as a cirrus, but as the "genital sinus" or "ductus hermaphroditus." To call the sac surrounding it a cirrus sac is then a misnomer. Since this structure surrounds the genital sinus, it seems more appropriate to refer to it as a sinus sac. This sinus sac in Hemiuridae certainly functions as a cirrus sac, and is probably homologous with the cirrus sac. The difference is, however, a distinct one. For the expression of the association of the sac with a common sex duct instead of with the male duct alone, it is felt that the term "sinus sac" is justified. It has already been used by the present author in an earlier paper (Manter 1925). Some such term seems all the more advisable in view of the fact that in Nicoll's genus Hemipera a true cirrus sac appears to be present, containing "not only the ductus ejaculatorius but also the pars prostatica" (Nicoll 1913:245).

HEMIURUS LEVINSENI ODHNER 1905

[Figs. 62–63]

From stomach, *Gadus callarias* (Cod)
From stomach, *Urophycis chuss* (Squirrel hake)

Species of the genus Hemiurus are among the most common trematodes of marine fish. Distinction between species is, however, rather difficult. Looss in 1907 perhaps drew the most careful lines between species. It has been customary, especially previous to 1907, to refer most specimens which are clearly Hemiurus to the species *appendiculatus*. Thus, Stafford (1904) lists *H. appendiculatus* from ten different fish of Canadian waters. His only comment is: "Suckers of equal size." Looss shows that true *H. appendiculatus* up to 1907 had probably been found only in *Alosa finta*. He adds the additional hosts, *Gadus euxinus* and *Mugil capito*, in the latter of which the parasite might be accidental.

The following are some of the most distinctive characters of *H. appendiculatus* as given by Looss: Ventral sucker about twice as large as oral sucker; ringing of the cuticula disappearing dorsally at about the level of the pharynx; cirrus sac elongate, reaching a length about 3/4 the diameter of the ventral sucker; anterior part of the seminal vesicle very muscular; coils of uterus can stretch relatively far into the tail appendage, and come near the ends of the ceca.

All of the material collected from the Mount Desert Island region and belonging to the genus Hemiurus apparently belongs to the species, *H. levinseni*. The almost equal size of the suckers, with the oral sucker slightly larger is a constant character and one which separates the species from *H. appendicualtus*, *H. communis*, *H. lühei*, and *H. rugosus*. Since all of Stafford's representatives of this genus collected from Canadian fish show this character, it is very probable that they should belong in this species rather than in *H. appendiculatus*. Odhner reports *H. levinseni* from *Gadus morrhua* f. *ovak*, *Cottus scorpius*, and "many northern fish." It seems to be the most common Hemiurus species in arctic marine fish. In temperate waters the other species showing larger ventral suckers and small oral suckers are common. Thus, Linton's *Dist. appendiculatum* from Woods Hole fish shows a sucker proportion of about 1 : 2.

Hemiurus levinseni also differs from *H. appendiculatus* in possessing a shorter prostate tube, in a more constantly retracted tail appendage into which the uterus does not commonly extend, and in the cuticular rings extending dorsally to the level of the ovary.

In the present material, as in Odhner's, the tail was almost always completely retracted. The ceca may enter the tail slightly. In a single specimen the tail was fully extended and in this case both the ceca and a portion of the uterus extended into it (Fig. 62). The genital pore is median just behind the mouth opening. The genital sinus is long, and in contracted specimens the prostate tube does not begin until about the level of the ventral sucker. This tube is long and more or less curved according to body contraction. The seminal vesicle is large and divided into two sections, the anterior of which is surrounded by a muscular coat. The sizes of the specimens vary from 0.7 mm. to 1.68 mm. in length. Eggs measurements of 23 to 26 by 10 to 13μ agree well with Odhner's measurements of 26 to 28 by 12 to 13μ.

Eighteen specimens were taken altogether from the stomachs of six squirrel hake examined. Eight specimens were collected from three cod.

Cooper (1915) reports this species encysted in the muscles of small herring.

Measurements on four typical specimens are as follows:

Length	1.68 mm.	1.12 mm.	1.06 mm.	0.99 mm.
Width	0.467	0.37	0.374	0.37
Oral sucker	0.176	0.176	0.142	0.159
Ventral sucker	0.188	0.17	0.136	0.142
Pharynx	91 by 91μ	91 by 74μ	68 by 62μ	85 by 74μ
Eggs	23 12μ	23 13μ		26 10–13μ

BRACHYPHALLUS CRENATUS (RUDOLPHI 1802) [Fig. 53]

From stomach and intestine, *Osmerus mordax* (smelt)
" " " " *Pollachias virens* (Pollack)
" " " " *Clupea harengus* (Herring)

Lander (1904) has described the morphology of this form in detail. His material was also obtained from the smelt. In the present collection thirteen specimens were obtained from the stomachs and intestines of three smelt. Two other fish examined did not contain the trematode. The worms usually occur in the stomach.

Looss (1907:158) expresses the view that the American form of this parasite represents a new species which he names *B. affinis*. He finds the chief distinction to be the elongate and less lobed condition of the vitellaria and that the host and geographical occurrence differ widely from the European *B. crenatus* from *Salmo salar*. Lander figures the vitellaria as about twice as long as wide in an extended specimen, and his description indicates that this is the usual condition. In regard to lobation of these organs, Lander says: "They are commonly slightly lobulated, though they sometimes have a regular oval outline." Cooper (1915) describes and figures one specimen from a small herring. This specimen agreed with *B. crenatus* in having definitely lobed vitellaria (right, four lobed; left, three lobed). He also points out that either gland may appear entire when viewed obliquely. He suggests that the herring may represent an intermediate host and that the trematode might be discovered in *Salmo salar* from America.

The present material from the smelt agrees with descriptions of *B. crenatus* (Rud.). It is probably the same species collected by Lander from the same host. The vitellaria, however, in my specimens from the smelt were always distinctly lobed (Fig. 53), usually one being four-lobed, the other three-lobed. In none of the specimens were the vitellaria noticeably longer than wide. On the basis of these thirteen specimens from the smelt, it would appear that the American species is not distinguishable from the European species, *B. crenatus*. For hosts of *Brachyphallus crenatus* Odhner gives: *Cottus scorpius*, *Pleuronectes limanda*, *Gasterosteus aculeatus*, *Ammodytes tobianus*, *Salmo salar* and *trutta*, and *Osmerus eperlanus*. Lander's material was from *Osmerus mordax* and *Anguilla chrysypa*.

The smelt from which the present material was collected occurred in large numbers, together with small cod and pollack beneath the fishing wharf at Manset. All these fish were about the same size and evidently had similar feeding habits. The same trematode, *Brachyphallus crenatus*, was obtained from the stomach of the pollack, *Pollachius virens*, but not from the cod. Specimens from the pollack agreed in every respect with

those from the smelt. They were relatively small and usually contracted. The vitellaria were constantly lobed. Four fish yielded eleven trematodes.

Eight or nine specimens were obtained from the examination of 28 herring (*Clupea harengris*). The much larger size of most of these trematodes gave the impression of a different species, but the details of anatomy agreed with *Brachyphallus crenatus*. Moreover, the sizes agree with known limits for the species (Odhner recording a variation of 0.8 mm. to 2.5 mm. in body length, while Olsson gives 5 mm. as maximum length). Cooper (1915) found one small specimen in the stomach of the herring. The present collection of large mature specimens from this host indicates that the herring is a normal host for the parasite and not, at least exclusively, an intermediate host as suggested by Cooper.

Only in material from the herring was variation in vitellaria shape noted. In these specimens, lobing of the vitellaria was not common. The characteristic four- and three-lobed condition was clearly evident, however, in one specimen. The material from the herring agrees in this respect with Lander's description, although an elongate condition of the vitellaria was not common.

LECITHASTER GIBBOSUS (RUDOLPHI 1802)

[Fig. 61]

From intestine, *Myxocephalus octodecimspinosus* (?), Sculpin

Looss (1907) gives the following synonyms for this species:

Distomum mollissimum Lev. 1881[1]
nec *Distomum mollissimum* Stoss. 1889
nec *Apoblema mollissimum* Lss. 1896

Odhner (1905) reports this species from various northern fish (including *Cottus scorpius*). He separates the species from *Lecithaster confusus* Odhner. This latter species has the following synonymy:

Apoblema mollissimum Lss. 1896
nec *Distomum mollissimum* Lev. 1881
Hemiurus bothryophorus Lss. 1899
nec *Distomum botryophoron*[2] Olss. 1868[3]

A single specimen was collected from the intestine of one fish out of eleven examined. Stafford (1904) reports a species as *Lecithaster bothryophorus* Olsson (=*Apoblema mollissimum*) from the salmon and herring.

[1] This date printed 1891 was evidently a misprint.

[2] Olsson originally spelled this name *botryophoron*, but the word has been very commonly referred to as *bothryophoron*. Lühe (1901) called the species *Lecithaster bothryophoron* using it as type of the genus Lecithaster. Odhner (1905) shows this species to be actually *Lecithaster gibbosus* (Rud.).

[3] Given as 1869.

Odhner (1905) assigned *Lecithaster bothryophorus* as the type of a new genus Lecithophyllum. As *Apoblema mollissimum* is a synonym of *Lecithaster nfusus*, the actual identification of Stafford's material which is undescribed is unknown. Linton (1901 and 1905) reports *Dist. bothryophoron* from various fish, but to which species of Lecithaster his form belongs cannot be determined from his descriptions or figures.

The two species *Lec. confusus* and *Lec. gibbosus* are closely related. The present specimen was assigned to the latter species because of the thickness of the ovarian lobes, the length of the vitelline lobes, and because the seminal vesicle did not extend posterior to the ventral sucker. According to Looss, these three points are the chief means of distinction between the two species.

Measurements on the specimen are as follows:

Length	1.12 mm.
Width	0.4
Oral sucker	0.17
Ventral sucker	0.256
Pharynx	0.09 by 0.09
Eggs	23 to 26 by 15μ

APONURUS SPHAEROLECITHUS MANTER 1925

[Figs. 70–74]

From stomach, *Urophycis tenuis* (Hake)

The genus Aponurus is considered by Looss (1907) as most nearly related to Lecithaster, although showing relationships to Brachyphallus. The only other species in the genus is *A. laguncula* Lss.

The trematodes of this genus are small in size (about one millimeter in length) and almost cylindrical in form, tapering anteriorly but broadly rounded posteriorly. The ventral sucker, located about 1/3 from the anterior end, is almost exactly twice the size of the oral sucker. The genital pore is about at the level of the pharynx. The genital sinus is surrounded by a conspicuous pear-shaped sinus sac. Vagina or metraterm is lacking or very short. Seminal vesicle rather short, swollen, mostly anterior to the ventral sucker. Testes, ovary, and vitellaria globular. The vitellaria are in two groups, one of four, another of three follicles. They are more or less spherical, and are located just posterior to the ovary. Coils of the uterus fill the body posterior to the vitellaria, but anterior to the ovary are more limited to the space between the intestinal ceca.

The genus Aponurus bears close relationship to Lecithaster and Lecithophyllum. Lecithophyllum was created by Odhner (1905) for Olsson's *Distoma botryophoron.* Odhner studied Olsson's type material. The following table, showing differences between the three genera is based on data as given by Odhner and Looss.

	Lecithaster	*Lecithophyllum*	*Aponurus*
(1)	Genital pore rather distant from oral sucker	Genital pore rather close to oral sucker	Genital pore rather close to oral sucker
(2)	Ovary 4-lobed	Ovary entire	Ovary entire
(3)	Posterior end tapering	Posterior end broadly rounded	Posterior end broadly rounded
(4)	Pars prostatica much longer than genital sinus	Pars prostatica shorter than genital sinus	Pars prostatic as long as genital sinus
(5)	Genital sinus reaching about to ventral sucker	Genital sinus reaching almost to ventral sucker	Genital sinus reaching only about half way to ventral sucker
(6)	Eggs small (15 to 25μ) thin-shelled	Eggs large (60μ) thick-shelled	Eggs small (26μ)
(7)	Vitellaria elongate in 7 connected parts	Vitellaria elongate in 7 connected parts	Vitellaria rounded in 7 separate parts

The significance to be attached to the distinctly separated nature of the follicles of the vitellaria might be questioned and perhaps should not be considered as of generic value. Looss himself brings up this question. In his discussion of Lecithaster he says (Looss 1907:161): "Einen gewissen Anklang an die bei den Verwandten herrschenden Verhältnisse kann man vielleicht darin erblichen, dass die 7 Schläuche nicht selten so gelagert sind, dass mehr oder weniger deutlich eine Gruppe von 4 und eine von 3 Schläuchen ensteht." Yet in Lecithaster and Lecithophyllum the follicles are described as distinctly united centrally. Again, Looss seems to express some doubt as to whether the vitellaria in Aponurus are all actually unconnected. He says (p. 168): "Bei der Pressung frischer Tiere geht die Kugel-form in eine Birn- oder Keulenform über, die Gruppen von 3 und 4 bleiben meist deutlich sichtbar, verschinden manchmal aber ebenfalls, und dann ähneln die Dotterstöcke vollkommen denen von Lecithaster, da die Schlauche alle von einem Punkt auszugehen scheinen. Ich glaube auch, dass dies tatsächlich der Fall ist, obwohl der direkte Nachweis an ganzen und aufgehellten Individuen wegen der ungünstigen Lagerung der Follikel nicht zu erbringen ist." Yet, if it be true that the vitellaria are actually as in Lecithaster then there is much less justification for separation of Aponurus from Lecithophyllum. The condition of the vitellaria in the present material will be discussed below.

Two specimens of this form were obtained from the stomach of one fish. These specimens agree in the main with the characters of the genus. Both seemed fully mature and their size measurements were 1.47 by 0.29 mm., and 1.1 by 0.245 mm. The greatest thickness is about the same as the greatest width, so that at the ventral sucker and posterior the worm is cylindrical. The body is broadly rounded at the posterior end. The cuticula is smooth and there is no tail appendage. The sucker proportion is almost exactly 1 : 2. Pre-pharynx lacking, pharynx globular; esophagus short; wide ceca reaching to the posterior end of the body.

The excretory system is as in other Hemiurids. Posteriorly it is concealed by egg masses. The unpaired vesicle branches between the ovary and testes, and the two lateral branches unite dorsal to the pharynx.

The genital pore is ventral, median, at about the level of the middle of the pharynx. The pear-shaped muscular sinus-sac extends dorsally and posteriorly from the pore and surrounds the genital sinus. It reaches about half way to the ventral sucker. In this posterior extent of the genital sinus the form differs from Lecithophyllum. The wall of the sac consists of an outer layer of longitudinal muscles and an inner layer of circular muscles. Between these layers and the sex duct is a space filled by parenchyma tissue containing a few cells. The width of this parenchyma-filled space is about equal to the combined thickness of the muscle layers. The common genital duct coils somewhat within the sac, at the posterior end of which it splits into the male and female sex ducts.

The testes are located a short distance posterior to the ventral sucker. In both specimens the right testis was slightly anterior to the left. Their size is relatively small, and in this respect they differ from the condition in *A. laguncula*, where the testes fill a large portion of the body cross-section. The seminal vesicle is large, and ovoid or simple-sac like in shape. In *A. laguncula* it is bent slightly at each end. In the present species it extends posteriorly to near the middle of the ventral sucker. In *A. laguncula*, it does not extend very far beyond the anterior margin of the sucker.

The duct of the pars prostatica leads from the ventral surface of the seminal vesicle near its anterior end, bends directly dorsally over the anterior end of the vesicle, reaches to the dorsal wall, and then bends again ventrally to unite immediately with the uterus to form the genital sinus. The wall of the duct is composed of small flat cells apparently without ciliary processes. The form of the pars prostatica is S-shaped in lateral view (Fig. 70), and the gland does not run directly posteriorly as in *A. laguncula*. The cells of the prostate gland are large in size and somewhat angular in shape. The total length of the gland is just about equal to the length of the sinus sac. Thus, in length it agrees with *A. laguncula* and differs from *Lecithophyllum botryophoron*. In a 2 mm. specimen of the latter species, the genital sinus was 0.3 mm. long and the pars prostatica 0.17 mm. or about 1/2 as long. In the 1.1 mm. specimen of *A. sphaerolecithus* the pars prostatica was about 0.19 mm. in length. In this same specimen the sinus sac was about 0.2 mm. in length measured from the lateral aspect. This proportional length is about as in Lecithophyllum, but due to the dorsal slant of the organ its posterior edge only reached a point about half way to the ventral sucker.

The ovary is located a short distance posterior to the testes and slightly to the right. It is spherical in form and smooth in outline. The globular

seminal vesicle is located anterior and slightly dorsal to the ovary. It is about one half the size of the ovary. Laurer's canal is absent.

The vitellaria consist of seven follicles, globular in shape a smooth with outline, and located close together just posterior to the ovary. They are in two groups. One group of four is located to the right and just posterior to the ovary, while the group of three is located to the left (Figs. 73–74). The follicles in the group of four are larger, being almost as large as the ovary. This size of the follicles is greater than in *A. laguncula,* where they are about one half the size of the ovary. The position of both ovary and vitellaria is near the ventral surface of the body. In regard to the separate or connected condition of the follicles, a series of sections through the larger specimen gave no indication that the follicles are united at any point. While some were in close contact with each other, others were clearly isolated. In spite of Looss's question, this condition seems definitely distinct, certainly from the normal condition in Lecithaster and from the condition described for Lecithophyllum. More material will be necessary to settle the point finally.

The coils of the uterus are as in *A. laguncula.* The terminal region of the uterus is surrounded by the cells of the prostate gland. The uterus runs close to the male duct in this region and with it swings dorsally over the anterior end of the seminal vesicle (Fig. 72). The male and female ducts do not unite outside the sinus sac. The male duct opens into the extreme posterior tip of the sac, while the female duct enters from the left at practically the same spot.

The eggs are very large and this character forms a conspicuous difference between the two species of Aponurus. Looss gives the eggs of *A. laguncula* as about 0.027 mm. in length and 0.016 mm. in width. Eggs in the present species were 0.056 to 0.065 mm. by about 0.026 mm. This size and the thick egg shell agree with Lecithophyllum.

Measurements are as follows:

Length	1.47 mm.	1.1 mm.
Width	0.296	0.245
Oral sucker	0.137	0.1
Ventral sucker	0.264	0.19
Ant. end to post. edge ventral sucker	0.617	0.43
Pharynx	63 by 63μ	57 by 57μ
Diameter, ant. testis	68μ	57μ
Diameter, post. testis	79μ	68μ
Diameter, ovary	91μ	85μ
Diameter, vitellaria	85 to 91μ	62 to 72μ
Eggs	58–62 by 26μ	56–65 by 26μ

GENOLINEA LATICAUDA MANTER 1925

[Figs. 64–66]

From stomach, *Hippoglossus hippoglossus* (Halibut)

Small to medium-sized forms, with flattened body tapering slightly anteriorly, at which end it is roundly pointed; body broadly rounded posteriorly. Body almost uniformly wide. Cuticula smooth. Tail appendage lacking. Oral sucker embedded in body, overlapped dorsally by fleshy lip. Ventral sucker about one and a half times the size of the oral sucker, located anterior to the middle of the body and about at the end of the first body third. No pre-pharynx, pharynx broad, esophagus very short, ceca broad, extending to posterior tip of body. Excretory system as in Hemiuridae, branches uniting dorsal to pharynx. Genital pore median, ventral, at about the level of the forking of the intestine. Testes compact, globular, obliquely behind one another some distance behind the ventral sucker. Ovary large, compact, globular, located behind testes. Vitellaria behind one another posterior to ovary, compact, globular. Uterus sends two lateral coils posterior to vitellaria to near body tip. Between ovary and ventral sucker the uterus is in large transverse coils. Genital sinus short, seminal vesicle much coiled, just anterior or slightly overlapping the ventral sucker. Eggs 28 to 31 by 12 to 15μ.

The Hemiurid affinities of this form are seen in the digestive and excretory systems, the general form, shape, and position of the gonads, the genital sinus, prostate gland, and oral lip. It is most closely related to Genarches Lss. and Derogenes Lühe. which are grouped under the Syncoelinae. It differs from both in body shape which is not markedly tapering at either end, and in position and proportional size of the ventral sucker which is distinctly anterior to mid-body. None of the three specimens showed contraction of the neck region, so that this sucker position can be assumed as normal. The course of the uterus in Genolinea is distinctly different than it is in either Genarches or Derogenes. Genarches is, of course, also clearly separated by the union of the two intestinal ceca posteriorly.

Genolinea, in addition to points already mentioned, is distinct from Derogenes in possessing a very short prostate gland, a much coiled seminal vesicle, and a more linear arrangement of the reproductive organs.

Measurements on two of the specimens are as follows:

Length	1.87 mm.	1.32 mm.
Width	0.336	0.299
Oral sucker	0.136	0.125
Ventral sucker	0.239	0.199
Ant. end to post. edge ventral sucker	0.617	0.5
Pharynx	57 by 79μ	57 by 74μ
Ant. testis	0.136 mm.	0.1 mm.

Post. testis	0.136	0.13
Ovary	0.165	0.15
Ant. vitellarium	0.114	0.12
Post. vitellarium	0.142	0.12
Eggs	31 by 13 to 15μ	28 to 31 by 12μ

GONOCERCA PHYCIDIS MANTER 1925
[Figs. 67–69]

From gills and branchial cavity, *Urophycis chuss* (Squirrel Hake)

Body elongate, both ends bluntly rounded, cuticula smooth, not ringed, body only slightly flattened, oval in cross-section, tail appendage lacking. Ventral sucker posterior to middle of body, almost twice as large as the oral sucker, about as wide as body. Mouth opening sub-terminal, overlapped dorsally by lip-like projection of body, oral sucker embedded in body. No pre-pharynx, short esophagus, intestinal ceca reaching to posterior end of body. Excretory vesicle branching just posterior to the ovary, the branches running forward laterally and uniting dorsal to the oral sucker near the anterior tip. Gonads crowded together posterior to the ventral sucker and filling most of the body space in that region. Genital aperture median and ventral, close behind mouth opening. Ovary median just behind ventral sucker, anterior to the testes. Vitellaria compact, unlobed, lateral and very slightly posterior to the ovary. Testes large, just posterior to the ovary, obliquely behind and in contact with each other. Ootype without membrane, dorsal and anterior to the ovary. Eggs comparatively large. Seminal vesicle comma-shaped, pointed anteriorly, located at about the level of the pharynx. Prostate gland little developed, free, short, located ventral to the oral sucker just anterior to the seminal vesicle. The covering of the seminal vesicle seems to be non-muscular, hence the cirrus sac is absent or at most weakly developed. There is a short genital sinus. No localized seminal receptacle. Region of the uterus just anterior to the ovary often crowded with sperm cells.

About 15 specimens were taken from the gills and branchial cavity of a single host. The fish had been caught but a few hours and it is possible that (as is true of some other Hemiurids) the gill region is the normal habitat of the parasite. Two specimens altogether, however, were obtained from the stomach of this fish.

That this trematode belongs to the non-appendiculate Hemiuridae there can be no doubt. Its features characteristic of the family are seen in the excretory system, projection of upper lip, position of genital pore, and character and form of the gonads. It differs from most members of the family in the reversed position of the ovary in relation to the testes. Still more marked distinctions are found in the location of the uterus entirely anterior to the ovary, in the position of the seminal vesicle far

distant from the ventral sucker, in the position of the prostate gland, and in the crowded localization of the gonads and vitellaria in the tail region.

The occurrence of the parasite on the gills and in the branchial cavity of the host is not unique among the Hemiuridae. Odhner gives the following as "gill parasites": *Accacoelium contortum,* Syncoelium, Otiotrema, Bathycotyle, and Liocerca. Of these forms, the present species resembles most closely Liocerca. Liocerca is also one of the few members of the family with testes posterior to the ovary. Gonocerca differs markedly, however, from Liocerca in the following points: position of the genital pore, which is considerably more posterior in Liocerca; position of the seminal vesicle, which is close to the ventral sucker in Liocerca; length of the prostate gland, which is elongate in Liocerca; and in uterine coils, which extend posterior to the ovary in Liocerca. Liocerca shows more resemblance to Hemiurus than does Gonocerca.

Nicoll in 1913 describes the genus Hemipera which he considers most closely related to Liocerca. It resembles this genus in inverted position of the ovary. In this respect, it is also like the present form with which it shows further similarity in position of the ventral sucker. The body form of all three genera is very similar. In Hemipera, the testes are lateral to each other, instead of behind one another, as in the other two genera. Hemipera shows the widest divergence in possessing a cirrus sac inclosing both prostate gland and seminal vesicle, and in having egg with polar filaments.

A tabular comparison of these genera follows:

	Liocerca	*Gonocerca*	*Hemipera*
Habitat	gills	gills	stomach
Position of genital pore	Somewhat distant from oral sucker	Close to oral sucker	Somewhat distant from oral sucker
Position of ventral sucker	About mid-body	Posterior to mid-body	Posterior to mid-body
Testes	Behind one another	Behind one another	Lateral to each other
Cirrus sac	Inclosing only male duct	Absent	Inclosing prostate gland and sem. ves.
Prostate gland	Free, elongate	Free, short	Inclosed
Seminal vesicle	Near ventral sucker	Near pharynx	Between suckers
Eggs	Numerous, non-filamented	Numerous, non-filamented	Few, filamented

Form, shape, size, cuticula, excretory and digestive systems are similar in all three genera.

Gonocerca differs from Derogenes in extent and position of prostate gland, position of genital pore, course of uterus, and inverted position of ovary in relation to testes. These same differences except extent of prostate gland separate it from Genarches.

Measurements on five specimens are as follows:

Length	1.8 mm.	1.9 mm.	1.3 mm.	1.4 mm.	1.4 mm.
Width	0.48	0.37	0.29	0.37	0.4
Ant. end to post. border ventral sucker	1.3	1.3	0.89	1.	1.
Oral sucker	0.26	0.22	0.18	0.2	0.22
Ventral sucker	0.43	0.37	0.29	0.33	0.35
Ovary	0.2	0.12	0.13	0.12	0.125
Testes	0.22	0.19	0.17	0.23	0.23
Vitellaria	0.15	0.1	0.1	0.114	0.114
Pharynx	114 by 85μ	80 by 80μ	74 by 85μ	96 by 51μ	85 by 79μ
Eggs		46 to 50 by 20 to 26μ			

DEROGENES VARICUS (MÜLLER 1784)

[Fig. 57]

From Stomach, *Gadus callarias* (Cod)
" " *Urophycis tenuis* (Hake)
" " *Urophycis chuss* (Squirrel hake)
" " *Anarrhichas lupus* (Wolf fish)
Intestine, *Hippoglossus hippoglossus* (Halibut)
" *Myxocephalus octodecimspinosus* (Sculpin)

This parasite is known as perhaps the most common marine fish trematode. It shows a very extensive host range, although usually present in small numbers. Nicoll reports mature specimens as small as one millimeter in length while Stossich gives a maximum length of 7 mm. The parasite is quite easily distinguished from other Hemiurids by its lack of tail appendage, position of ventral sucker posterior to middle of the body, small terminal sinus sac inclosing both sex ducts, its long prostate, and large eggs. There is no pre-pharynx. The genital opening is about at the level of the branching of the intestine. Gonads are similar to those of the typical Hemiurids. Measurements on an average sized specimen from the cod were:

Length	1.7 mm.
Width	0.5
Oral sucker	0.22
Ventral sucker	0.37
Ovary	0.14 x-diameter
Testes	0.14 x-diameter
Pharynx	85× 85μ
Eggs	50×28–30μ

Stafford (1904) names a new species *Derogenes plenus* briefly described from the wolf fish. The single specimen from that host in the present collection showed no specific difference from *D. varicus* and there appeared no justification for assigning it to a different species. Whether or not it represents Stafford's form is, of course, unknown; but in view of the meager description of *D. plenus* the species seems somewhat uncertain.

*HIRUDINELLA FUSCA** (POIRIER 1885)
[Figs. 75–79]

Synonyms: *Dist. fuscum* Poir.
Dist. verrucosum Poir.
Dist. clavatum of Linton
From Stomach, *Xyphias gladius* (Sword fish) Woods Hole

This trematode belongs to the interesting group of large forms represented by *Dist. clavatum.* Considering the early discovery and long history of trematodes of this group, precise knowledge of their internal structure is rather meager. The history and synonymy of the group has been given by Poirier (1885), Buttel-Reepen (1903), and Mühlschlag (1914) and will not be discussed here. The group itself is well isolated (although referred to by Odhner as representing a sub-family of the Hemiuridae), yet the species within it are remarkably similar. The early custom of dependence on external features has led to confusion and uncertainty of species. Poirier's work (1885), while dealing in detail with the morphology of the group, does not bring out clear distinction between species. The later work of Buttel-Reepen and Mühlschlag has separated with considerable definiteness the following species which evidently should all be referred to the genus Hirudinella: *Dist. clavatum, Dist. ampullaceum, Dist. seimersi, Dist. fuscum,* and *Dist. ingens.* The *Dist. insigne* of Poirier is a synonym of *Otodistomum veliporum,* and his *Dist. verrucosum* is considered by Mühlschlag as identical with *Dist. fuscum.*

In his various papers from Woods Hole, Linton records *Dist. clavatum* from the stomach of *Xyphias gladius.* He describes the form to some extent in his 1896 paper. Cooper (1915) identifies as *Hirudinella clavata* trematodes collected from the stomach of *Thunnus thynnus* in Canadian waters. The present material from *Xyphias gladius* at Woods Hole is very probably the same form recorded by Linton. Since Linton's description is incomplete and since the more recent work of Mühlschlag emphasizes new specific characters in the genus, a brief description of this form might be of some importance.

One vial of the material contained 60 specimens varying from 7 to 23 mm. in length and from 2.5 to 5 mm. in width. The body is very robust, stout, thick, and very cylindrical especially posterior to the ventral sucker. The posterior end is broadly rounded. The neck region is smaller than the swollen hindbody, and in a 23 mm. specimen measured about 6 mm. in length. The body is marked by transverse folds or wrinkles characteristic of the group and due to body contraction. The ventral sucker is very prominent with wide, sometimes wrinkled or corrugated margins. Its width is often greater than the width of the body (Figs. 76–77). In a

* Collection of Dr. H. B. Ward, vials Nos. 13.44 and 13.45.

12 mm. specimen, the oral sucker was 1.17 mm. in diameter, the ventral sucker 2.19 mm., and the pharynx 0.64×0.42 mm.

The extraordinarily thick body wall is made up of (1) a thick cuticula, (2) a "sub-cuticular" layer in which occur (especially in the neck region) circular and longitudinal muscle fibers, (3) a thick circular muscle layer, and (4) an inner layer of longitudinal muscles. Internal to this last layer there occurs a well-defined cellular layer which has been called the sub-cuticular cellular layer. The condition of these layers were found as reported by Mühlschlag. The circular layer is more prominent anteriorly. In the mid-body regions the longitudinal layer is enormously developed and the fibers are grouped into conspicuous bundles. This layer may represent the internal parenchyma muscles of Otodistomum and Azygia.

The oral sucker opens directly into the pharynx. There is a strongly developed esophagus which, in contracted specimens, leads dorsally and anteriorly from the posterior end of the pharynx. The esophagus splits before losing its cuticular lining, and the lumen of each branch expands into a roomy tube. These two esophageal expansions open into the anterior regions of the intestinal ceca. Here the ceca are modified into swollen, bulb-like regions characterized by cells with extremely long, cilia-like processes which practically fill the wide lumen. These modified regions have been called glandular. They lead abruptly into the ceca proper which are lined with small cells having short, cilia-like processes. The ceca stretch to the posterior end of the body, and become very large in regions posterior to the ventral sucker, filling the greater part of the large body of the worm. Considerable amount of black food substance occurs within the intestinal ceca.

Excretory vessels permeate all regions of the parenchyma, so that almost any section through the trematode shows cross-sections of numerous tubes of this system. There is an unpaired excretory vesicle extending as a laterally flattened tube between the two enormous ceca. This vesicle opens to the exterior through a short duct provided with circular, longitudinal, and oblique muscles. The plexus of accessory excretory tubes is very complicated. The unpaired vesicle divides into two branches just behind the posterior limit of the uterus and vitellaria, or about half way between the posterior and anterior ends of the body. The lateral branches evidently wind and bend extensively, and the accompanying plexus of various sized vessels continue into the region of the oral sucker.

The genital pore is median, ventral, and nearer the oral sucker (Linton gives its position as mid-way between the suckers). In material of the present studies it occurred about opposite the posterior end of the pharynx. It leads into a very large genital atrium which is somewhat flattened parallel with the ventral body surface (Fig. 75). The genital opening is near the anterior limit of this atrium. A conspicuous genital papilla

projects into the atrium from its dorsal surface and on the truncated tip of this papilla the male sex duct opens. The vagina does not enter the papilla. Its opening is posterior to this papilla and separated from it by a depression in the atrium wall. This widely separated position of the openings of the sex ducts into the atrium is characteristic for *H. fusca* and Figure 75 shows almost exact agreement with Mühlschlag's diagram of that region. In *H. clavata,* the two ducts open close together on a common papilla (Poirier 1885).

The testes lie obliquely behind one another close behind the ventral sucker which they may slightly overlap dorsally. The somewhat coiled seminal vesicle leads into the duct of the large prostate gland. The prostate gland is lined with cells bearing cilia-like processes. The prostate gland coils slightly. At the base of the genital papilla the duct changes abruptly into the ejaculatory duct. This duct possesses a very thick inner coat of cuticula, and a powerful layer of circular muscles. It is, moreover, provided with numerous muscles which attach themselves to its outer wall These muscles run obliquely through the papilla, and dorsal to it some of them are seen to lead anteriorly to the longitudinal body muscles of the dorsal side. Others, leading posteriorly, split off from the longitudinal muscles of the uterus. Still others seem to be connected with longitudinal body muscles of the ventral and lateral sides (Fig. 79).

In *Dist. ingens* and *Dist. ampullaceum* where the two ducts open in common, special musculature surrounds not only the ejaculatory duct but also the terminal region of the vagina. This common muscular system surrounding both ducts was called a cirrus sac by Buttel-Reepen (1903), but that it could not be correctly interpreted as such was pointed out by Mühlschlag who called it the "genital musculature." This condition of both sex ducts being surrounded by a common musculature brings to mind the so-called "cirrus sac" about the genital sinus in some Hemiurids. Homologies would be difficult to draw, however, since the genital sinus in the latter case is probably a composite of the true genital atrium and the fused sex ducts.

The ovary is located just posterior to the testes. The ootype lies in contact with it posteriorly and ventrally. Both organs are surrounded by a fibrous membrane some of the fibres of which seem to bind the two together as in Otodistomum. The left vitelline duct runs between the ootype and ovary to unite with the right duct somewhat to the right of the middle line. The common vitelline duct penetrates the ootype anteriorly. It unites with the oviduct within the ootype. Laurer's canal also penetrates the membrane of the ootype. It enters more toward the posterior, although likewise from between ovary and ootype. This canal is very powerfully developed with a cuticular lining and a thick wall of circular muscles. It is unusually long, since the ootype is near the ventral

surface and the canal opens to the exterior dorsally at about the level of the ovary. After its penetration into the ootype, it opens into a swollen, bulb-like enlargement which lacks the muscular coat. This swollen region in turn leads into a narrow duct which opens into the oviduct slightly before the vitelline duct (Fig. 78). The thin-walled enlargement of Laurer's canal seems to be morphologically a true seminal receptacle. No spermatozoa, however, were seen anywhere along the length of the canal.

The uterus coils posteriorly between the intestinal ceca to a point about half way between anterior and posterior ends of the worm. It then coils anteriorly, extending dorsal to the ovary and testes, ventral to the seminal vesicle, and opening into the atrium as already indicated. At about the level of the ovary the character of its wall changes and includes circular and longitudinal muscle layers, and, outside the latter, a dense layer of small coils of supposedly glandular function. Overhanging, lip-like folds of the atrium about the opening of the vagina may serve as a valve to prevent re-entrance of eggs into the vagina from the atrium which is often well filled with them. Furthermore, out-pocketings of the vagina close to its tip results in forming a second valve-like fold within the vagina itself (Fig. 79). The constancy of this structure is, however, unknown.

The vitellaria are tubular and winding. They occur laterally on each side of the body. Anteriorly they reach to about the level of the testes, and posteriorly as far as the posterior extent of the uterus. The rather thin-shelled eggs are broadly ovoid and measure about 32 by 25μ.

From the morphological features discussed above, it is evident that the species must be referred to *H. fusca*. Most characteristic is the nature of the genital atrium. Mühlschlag gives also the following specific characters: the short, thick-set body form; the swollen borders of the ventral sucker; and the bulb-like swelling of Laurer's canal within the ootype.

*SIPHODERA VINALEDWARDSII** (LINTON 1899)

[Figs. 80–83]

From *Opsanus tau* (Toad fish), Woods Hole
Synonym: *Monostomum vinaledwardsii* Lint. 1899

This form was first named and imperfectly described as *Monostomum vinaledwardsii*. This original material was obtained by Linton, also from the toad-fish at Woods Hole. In 1911 Linton found further material of the same species from *Ocyurus chryurus* at Tortugas. He corrects and extends his former (1899) description and places the form in a new genus (Siphodera) of the distomes. This genus with a few other genera from the same region (Tortugas) he includes in the new family Siphoderidae.

The present form agrees very largely with Linton's later description. As he was, however, uncertain in regard to some points, the form will be briefly described here.

*Collection of Dr. H. B. Ward, vials no 22.217, 22.218.

The body shape is broadly oval in outline and somewhat pointed at each end. It is somewhat flattened but is thicker in the middle regions. An average sized specimen measured 1.88 mm. in length, 1.33 mm. in width, and 0.53 mm. in greatest thickness, which was through the region of the ventral sucker. The body surface is covered with minute scale-like spines. The circular oral sucker is at the anterior end. In regard to the ventral sucker, Linton (1911) says: "The ventral sucker is a part of the genital apparatus (cirrus) and is depressed in a circular pit of the body wall. The border of the pit is muscular and has strong muscular fibers radiating from it." This description applies to the position of the ventral sucker, the bordered pit and radiating muscles being conspicuous even in toto-mounts, but the sucker itself has no direct connection with the genital system. The common opening of the sex ducts is just anterior to the sucker and just within the border of the pit (Fig. 83), as will be shown later. The sucker is therefore referred to in this paper as the ventral sucker instead of using Linton's term "genital sucker." This sucker is smaller than the oral sucker, and is located a little less than 1/3 the body length from the anterior end. In a 1.8 mm. specimen the oral sucker measured 0.2 mm. in diameter and this ventral sucker only 0.09 mm. The diameter of the genital pit (which incloses both the genital pore and the ventral sucker) was 0.16 mm. The ventral sucker may be protruded from the pit (Fig. 82). There is a short pre-pharynx, globular pharynx, and short swollen esophagus. The intestinal ceca are widespread and reach almost but not quite to the posterior tip of the body.

The excretory system is very simple. The unpaired excretory vesicle occupies a large part of the central region of the hind-body. It opens at the posterior end through a short duct which is surrounded by deeply staining cells. Just posterior to the ovary or not far behind the ventral sucker, the vesicle splits into two lateral branches which continue forward and end blindly beside the oral sucker. They occur internal to the intestinal ceca, cross them ventrally in the region of the esophagus, and run on each side of the pharynx.

The musculature of the body wall is poorly developed. There is a weak circular layer and a longitudinal layer of somewhat separated bundles. The powerful diagonal muscle bands which run out obliquely and laterally from the border of the genital pit seem to originate in the neighborhood of the longitudinal body muscles. The ventral sucker is provided with two strong muscles which are attached to its outer border laterally and lead almost directly dorsally to the region of the seminal vesicle (Fig. 82). The body parenchyma is very loose and open.

The testes are in two groups in the lateral regions of the middle of the body. The number is variable, usually 4 or 5 on each side. They are located near the dorsal surface, so that ventrally they are considerably

concealed by the egg-filled coils of the uterus. The seminal vesicle is median in position, anterior to the testes, with its anterior limit over-reaching the posterior border of the ventral sucker. It is swollen tube-like in form and slightly coiled. Its walls are quite thick and evidently muscular, although the direction of the fibers could not be made out. At about the level of the ventral sucker it bends ventrally and is constricted off (by an inward continuation of its wall) from a succeeding bulb-like portion (Fig. 83). This latter region leads ventrally tapering, carrot-like. Its outer wall is also heavy like that of the seminal vesicle. The distal portion represents the ejaculatory duct. A short distance before it reaches the genital pore, it is joined ventrally by the vagina. The common opening is very close in front of the ventral sucker and within the anterior border of the genital pit. The distal bulb-like region of the male system is evidently what Linton referred to as "the prostatic portion of the cirrus pouch." Its inner wall is lined by what seems to be a layer of tall delicate cells, but these were indistinct and no nuclei could be made out. From material at hand, which seemed to be in good condition, it could not be definitely concluded that this region was glandular. As Linton studied fresh material, and as the cells in this region show very prominently in his figure (Linton 1911), his conclusion is probably correct.

The ovary is a much lobed organ located near the ventral surface a short distance posterior to the ventral sucker or about at the level of the posterior end of the seminal vesicle. The vitellaria are composed of numerous small follicles located nearer the dorsal surface and extending laterally across the body in the region between the ventral sucker and the anterior testes.

Linton's description is somewhat incomplete in regard to the region of the oviduct. Laurer's canal is present. It follows a practically straight course from the dorsal surface to the oviduct. Just before it enters the oviduct, it enters the very large, spherical seminal receptacle. This conspicuous organ is located just dorsal to the ovary and between it and the posterior end of the seminal vesicle (Fig. 83). The common vitelline duct is long, and enters the oviduct shortly beyond the entrance of Laurer's canal. The relations of these ducts are shown diagrammatically in Figure 81. A few small cells about the oviduct in this region probably represent a poorly developed ootype. The uterus coils posteriorly on the left side of the body, returning on the right. When it has returned to about the level of the ovary, it extends across the body and proceeds anteriorly on the left side of the seminal vesicle to join the ejaculatory duct. There is a very short genital sinus. The eggs measure 22 by 10 to 12μ.

The large pyriform cells in the cortical parenchyma region of the anterior part of the body were noted. Linton suggests that they represent

yolk-forming cells, but present material offered no evidence as to their function.

*DEROPRISTIS INFLATA** (MOLIN 1859)

From intestine, *Anguilla chrysypa,* Woods Hole.

This well-known parasite of the eel has already been clearly and fully described by Odhner (1902). The only other species in the genus is *D. hispida* (Rud.) from the sturgeon. Stafford (1904) records *D. inflata* from the eel, but Linton does not report it from Woods Hole.

The lateral expansions of the neck region are very characteristic for the genus. The body is covered with spines which are larger on the neck expansions and on a hump-like region on the dorsal surface opposite the pharynx. Odhner sees in the spined neck-expansions the fore-runner of the spined collar of Echinostoma. The two suckers are small and about equal in size. The testes are located in the extreme posterior end of the body, the ovary being about in the mid-body region. The vitellaria of small follicles extend in lateral and dorsal body regions from a point about half way between the ovary and ventral sucker to the anterior end of the anterior testis. The genital pore is median close in front of the ventral sucker. The genital sinus is tube-like. Both cirrus and vagina are prominent and armed with spines as in Stephanochasmus, a related genus.

The number of neck spines could not be counted, but the species can be assigned to *D. inflata* on (1) body size, (2) relatively short genital sinus, and (3) egg size. The body size varied from about 0.8 mm. to 4. mm. The genital sinus has a length about equal to the diameter of the ventral sucker. The egg size was 43 to 48 by 20 to 22μ.

ACANTHOCOTYLE VERRILLI GOTO 1899

[Figs. 86–88]

From Body surface, *Raia erinacea* (Bonnet skate)

A single specimen of a trematode which seems to belong to this species was obtained from *Raia erinacea.* The parasite was found in the content of the spiral valve but this was, of course, an accident. It is an ectoparasitic form. The species was described by Goto in 1899 from a single specimen sent him by Verrill who obtained it from the surface of a "skate" (from Cape Cod).

In regard to general shape and form, Goto (1899:284) says: ". . . . the body is of almost uniform breadth, and presents a slightly concave border anteriorly. There is also a distinct constriction at the level of the pharynx. The posterior sucker is large and circular, and has 34 radii consisting of

* Collection of Dr. H. B. Ward, vials no. 22.217 and 22.218.

* Collection of Dr. H. B. Ward, vial no. 13.72.

numerous hollow chitinous hooks. These radii leave the central area of the sucker free, and the most posterior four or five pairs gradually decrease in length backwards, so that there is a backward extension of the central area. The longest radii consist of about eleven hooks and the shortest of only four." This description of body shape, and posterior sucker fits the present specimen exactly, except that the posterior sucker of the latter has 32 radii of hooks. But Goto's figure shows 32 instead of the 34 described in the text, so that this latter number is probably a misprint. In regard to the small accessory sucker, Goto says: "At the hind end of the posterior sucker there is, in the median line, a roundish appendage armed with filiform chitinous hooks somewhat like the upper part of an interrogation point. I cannot exactly state the number of these hooks, but I counted more than twenty." These hooks were very clear in my specimen. There were 14 hooks arranged about the circumference of the sucker and two larger hooks in the center (Fig. 87). The body size of my specimen was 3.3 mm. by 0.93 mm. The diameter of the posterior sucker was 1.33 mm. and that of the accessory sucker 0.1 mm.

Goto claims that the anterior suckers are absent in this species and that "their places are occupied by two invaginations of the investing membrane of the body. . . . . The invaginations are narrow and deep, and appear like slits in the mounted specimen" (p. 284). He claims a similar condition for *A. lobianchoi* and believes Monticelli mistaken in referring to the invaginations as suckers. Monticelli (1904:73–74) disagrees with this view, pointing out that suckers are actually present but often quite completely retracted. Monticelli, in studying many individuals of this genus, found most varying appearances of the suckers due to contraction. The complete embedding of the suckers in the body by contraction is a very common reaction to the killing solution. Monticelli interprets Goto's figure as showing this condition. Study of my specimen supports Monticelli in this view. The elongate suckers with lip-like borders were clearly separate, especially at their margins, from the body wall although the internal boundaries of the suckers were indistinct.

The mouth is median and ventral about 0.26 mm. from the anterior end. It leads directly into a large, somewhat triangular-shaped pharynx. No esophagus could be seen. The intestine branches immediately and the ceca extend to the posterior end of the body.

There are about 52 testes. The exact number was difficult to determine as some of these organs were so close together as to seem double in nature Goto gives the number as only 37. The number is probably variable. They fill the inter-cecal space of the body in the posterior two thirds of its length. The seminal vesicle shows the regions characteristic of the genus.

The ovary is spherical. It is located about 1/3 from the anterior end and slightly to the left. The two vitelline ducts lead to a point at its

anterior end. The vitellaria are extensive and well developed. They consist of large compact follicles, flattened against each other longitudinally. They are located laterally on each side of the body, and partially surround and conceal the intestinal ceca.

Monticelli (1904) questions Goto's observations on the sexual openings. Goto himself says (1899:285): "The terminal portions of the genital ducts could not be satisfactorily made out in the single specimen at my command." Goto figures a single, common genital pore on the right side of the body in the neck region. There are, however, normally in this genus three sexual openings, one lateral opening of the metraterm, while the male aperture is close to the opening of the vagina in a more median position (cf. Monticelli 1899, Tav. 1, fig. 6; Tav. 2, figs. 29–31). Monticelli (1904: 71–72) concludes from Goto's figure and description that actually . . . . "the mouths of the genital ducts are arranged, fundamentally, as in all the other species of the genus." My material shows Monticelli to be correct. The male aperture is very close to the opening of the vagina at about the level of the forking of the intestine and slightly to the right. What Goto interpreted as the common genital pore is actually the opening of the metraterm. It is located laterally on the right side of the body. From it protrudes in my specimen a cluster of three eggs. These eggs are bright yellow in color and measure 0.428 by 0.085 mm. The stalk-like basal region of the eggs was inserted in a swollen terminal region of the metraterm.

Monticelli (1904) also expresses the conviction that Goto was wrong in regard to the metraterm opening to the right of the ventral face, believing that further study would show it to be on the left as in other species of Acanthocotyle. He suggests that Goto might have confused the dorsal with the ventral surface. In my specimen there is no doubt, however, that the pore is on the right side. The mouth opening could be made out so that the ventral surface was definitely ascertained. There remains the possibility that both my specimen and that of Goto represent cases of amphitypy, as, indeed, Monticelli suggests might occur in this group as found by Cerfontaine (1900:449) so common among the Octocotylides. Only more abundant material can settle this point.

DACTYLOCOTYLE MINOR (OLSSON 1868)
[Figs. 84–85]

Synonyms: *Octobothrium palmatum* S. *minor* Olss. 1868.
Octobothrium minus Olss. 1876.
From Gills, *Urophycis chuss* (Squirrel hake)

This species was first named by Olsson (1868:18) as a variety of *O. palmatum* Leuckart. In 1876, Olsson (1876:10) named it *Octobothrium minus* n. sp. Cerfontaine (1898:302) observed that this species was prob-

ably a true Dactylocotyle species. Saint-Remy (1898:55) listed it as "*Dactylocotyle minor* Olss." Stiles and Hassall (1908) list the species as "*Dactylocotyle minor* Saint-Remy." As Olsson's original description of *O. palmatum* f. *minor* is fairly complete and accompanied by a figure, and since sub-specific names follow the same rules as specific names, there can be no reason for not retaining Olsson's original name *minor*, as Saint-Remy, in fact, did. The correct name is then *Dactylocotyle minor* (Olss.) Saint-Remy.

The following is a diagnosis of this species as given by Saint-Remy (1892:41): "Body flattened, divided into two parts by a deep indentation; anterior part lanceolate-oval, the posterior or caudal part much shorter than the anterior, provided with canals, carrying on each side 4 marginal pediceled suckers, pedicels cylindrical, equal. Testes in the median anterior part. Length 3 to 6 mm., width 1.5 mm. On gills of *Gadus melanostomus*."

Three specimens were collected from the gills of a single fish. Examination of numerous other fish showed no infection, so the parasite is probably not a very common one. In some respects the form seems to differ slightly from *Dact. minor*, but in view of the fact that body contraction partly explains these differences and that only three specimens were collected, they are referred to this species.

Stafford records *Dactylocotyle phycidis* from the gills of the squirrel hake in Canada. Considering the identity of region and host, it is probable that he was dealing with the form now being considered. The species cannot be referred to *Dact. phycidis* (although the hosts are similar) because of its marked difference in size, shape, and number of hooks in the genital sucker. It is like *Dact. palmatum* in possessing a common genital opening, 14–16 hooks in the genital sucker, and in having few non-filamented eggs in the vagina. Olsson's variety *Dact. palmatum minor* differs from *Dact. palmatum* in its smaller size and in the sharp division of its body into two regions.

In my material, the posterior region bearing the pediceled suckers or pincers was so distinctly cut off from the body proper as to appear appendicular (Fig. 84). Except for small branches from the intestine which invade this posterior part, all the organs are located in the anterior region.

The anterior region is flattened and broadly oval in shape. In life it is of a gray color. The surface of the body is not entirely smooth, and in this respect my material differs from the descriptions of all other representatives of the genus. Minute scale-like plates give the body a roughened surface particularly in posterior body regions and on the pedicels of the suckers. These scales are less conspicuous anteriorly where the body seems quite smooth.

Other features are in accord with descriptions of the genus. The posterior suckers are provided with a very complicated system of chitinous

supporting rods which make the suckers more like pincers in function. On each side of the mouth which is at the anterior tip of the body there is a small lateral sucker. A globular pharynx is present. The ceca of the intestine are profusely branched and the fine branches ramify throughout the whole body.

The genital pore is located on the ventral surface about 0.3 mm. from the anterior end. Its position can be located by the conspicuous genital bulb or sucker. This sucker actually surrounds the distal portion of the male duct. It is provided with a ring of 14 hooks (Fig. 85). The number of hooks in the genital sucker varies within narrow limits in a species. The testes are numerous. Packed closely together, they fill most of the mid-body region of the anterior part of the worm. The seminal vesicle is located far forward, dorsal and slightly posterior to the genital sucker. It is much coiled. Between it and the genital sucker is a swollen, bulb-like region with very thick walls. This structure is about the size of the pharynx near which it is located.

The compact and dense follicles of the vitellaria fill the sides of the body and almost meet just anterior to the ovary. The ovary is slightly but tightly coiled so that it is compact S-shaped. There is a large coiled seminal receptacle located slightly anterior to the ovary. An ootype and small yolk reservoir lie ventral to the ovary. The uterus leads a straight course anteriorly and joins the male duct ventrally outside the genital sucker and close to the genital pore. Only one non-filamented egg was found in the uterus.

Measurements on two specimens are as follows:

Length	2.8 mm.	2.9 mm.
Width	1.6 mm.	1.75 mm.
Oral sucker	0.108	0.114
Genital sucker	0.074	0.085
Egg	0.159 by 0.017	
Longest diameter of posterior suckers—1	0.188	0.199
2	0.245	0.21
3	0.381	0.228
4		0.399

SUMMARY AND CONCLUSIONS

A general collection of entozoa of marine fish was made at Mt. Desert Island, Maine. Of these parasites, the trematodes were selected for study.

Particular attention was given to *Otodistomum cestoides* from the stomach of *Raia stabuliforis*. The morphology of this form was studied in considerable detail and compared with *O. veliporum*, material of which from *Raia binoculata* was available. The two species were found to be even more similar than hitherto recorded, but were distinct in a marked difference in egg size. The extent of the vitellaria varied considerably and this feature cannot be used to separate species in this genus. The internal longitudinal parenchyma muscles were found to be somewhat scattered in these forms, but definitely external to the vitellaria, a condition to be contrasted with their position in the related genus, Azygia. The prominent genital papilla hitherto considered as a permanent structure in Otodistomum was found to have the capacity (in both species) of being completely flattened out, or completely protruded. It was found to be usually much less prominent in *O. veliporum*.

The growth changes of *O. cestoides* within its final host were studied from measurements on over 200 specimens. Conspicuous changes in size are associated with regional changes in body proportions. Growth results chiefly in body elongation and occurs chiefly posterior to the ventral sucker. The region of the uterus slightly increases its size ratio to other body parts after sexual maturity, but the tail region alone also maintains a constant proportional growth increase as compared with the region anterior to the ventral sucker. The two suckers maintain a constant proportional size in respect to each other. Both suckers are relatively much larger in young forms.

Live miracidia of *O. cestoides* were readily obtained by the hatching of eggs secured from adult worms. These eggs at the time of deposit contain mature larvae ready to hatch. The egg shell is, however, very thick. It was discovered that the hatching of the eggs was stimulated by evaporation of the sea-water in which they were kept. Eggs in cultures submerged in aquaria did not hatch. Larvae were obtained as early as five hours after removal of eggs from the worm. All indications point to the conclusion that the eggs do not normally hatch until eaten by the intermediate host.

The miracidium of *O. cestoides* was found to be unciliated. Its form and shape vary with the worm-like extension and contraction of the body. The anterior end of the larva is continually being retracted and extended

like a proboscis. The miracidium has no apparent capacity for locomotion. A conspicuous internal organ of the miracidium has been commonly interpreted as an intestine. It was found that this organ was four-partite in structure. Each part evidently consisted of one cell with a large nucleus. The organ therefore cannot be regarded as an intestine, but probably represents a group of unicellular glands.

The eggs of *O. cestoides* are eaten by snails kept in the same vial with them. This eating of the eggs was conspicuous only in the case of the common gasteropod, *Littorina littorea.* Larvae were found hatching in the intestine of this snail in two cases.

The entire family Azygiidae was studied in an attempt to clear up an evident confusion in that group especially in American forms. The type material of most American species of Azygia and related genera was studied. It was found that all American representatives (consisting of eleven recorded forms) could all be referred to three species of Azygia as follows: *Mimodistomum angusticaudum* Staff. and *Azygia loossii* Marshall and Gilbert to *Azygia angusticauda* (Staff.); *Dist. longum* Leidy, *Dist. tereticolle* of Leidy, *Megadistomum longum* (Leidy), *Azygia tereticolle* of Stafford, *Azygia sebago* Ward, *Azygia bulbosa* Goldberger, *Hassallius hassalli* Goldberger, and *Azygia lucii* of Cooper to *Azygia longa* (Leidy). *Azygia acuminata* Goldberger was retained. Apparent differences between many of the forms were found to be in accord with growth changes which would be expected in the group. *Azygia perryii* was also studied and found to be probably identical with the European species, *Azygia lucii.*

A general study was made of the entire trematode collection from Mount Desert Island. A few forms from Woods Hole are also considered. Twenty different species belonging to eighteen different genera are identified. A number of these are described at some length.

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EXPLANATION OF PLATES

With the exception of Figs. 3, 76, 77, and 81, all figures were drawn with the aid of a camera lucida. The scale projected is equal to 0.1 mm. unless otherwise indicated in the explanation of figures. The following abbreviations are used:

a	tail appendage	*lm*	longitudinal muscles
ac	accessory sucker	*mf*	meridional fibers
as	anterior sucker	*mo*	male sex opening
c	cuticula	*o*	ovary
cd	common sex duct	*od*	oviduct
cm	circular muscles	*ot*	ootype
cs	cirrus sac	*ov*	ovum
dm	diagonal muscles	*p*	genital papilla
dp	duct of prostate gland	*ph*	pharynx
e	excretory system	*pp*	prepharynx
ef	equatorial fibers	*pr*	prostate gland
ej	ejaculatory duct	*rf*	radial fibers
es	esophagus	*s*	spermatozoa
f	genital fold	*sr*	seminal receptacle
fo	female sex opening	*sv*	seminal vesicle
ga	genital atrium	*t*	testis
gc	gland cell	*u*	uterus
gp	genital pore	*v*	vagina
gs	genital sinus	*vs*	ventral sucker
i	intestine	*vt*	vitellaria
lc	Laurer's canal	*yd*	yolk duct

PLATE I

EXPLANATION OF PLATE I

Fig. 1. *Otodistomum cestoides*. Ventral view of adult. Scale = 1 mm.
Fig. 2. *O. cestoides*. Ventral view of young specimen.
Fig. 3. Copy of Nicoll's figure of cercaria of *O. cestoides* from cyst from flounder. Enlarged to same proportion as Figure 2.
Fig. 4. *O. cestoides*. Ventral view of young specimen. Scale = 1 mm.
Fig. 5. Sagittal section through anterior region of *O. cestoides* showing normal condition of genital papilla. Scale = 1 mm.
Fig. 6. Same, with genital papilla protruded. Scale = 1 mm.
Fig. 7. Sagittal section through genital atrium of *O. veliporum*.
Fig. 8. Same of *O. cestoides*.
Fig. 9. Sagittal section through a position of ventral sucker of *O. cestoides*.
Fig. 10. Frontal section through pharynx region of *O. cestoides*. Scale = 1 mm.
Fig. 11. Cross-section through edge of ovary of *O. veliporum* showing beginning of oviduct.
Fig. 12. Sagittal section through portion of body wall of *O. cestoides*. Scale = 0.5 mm.

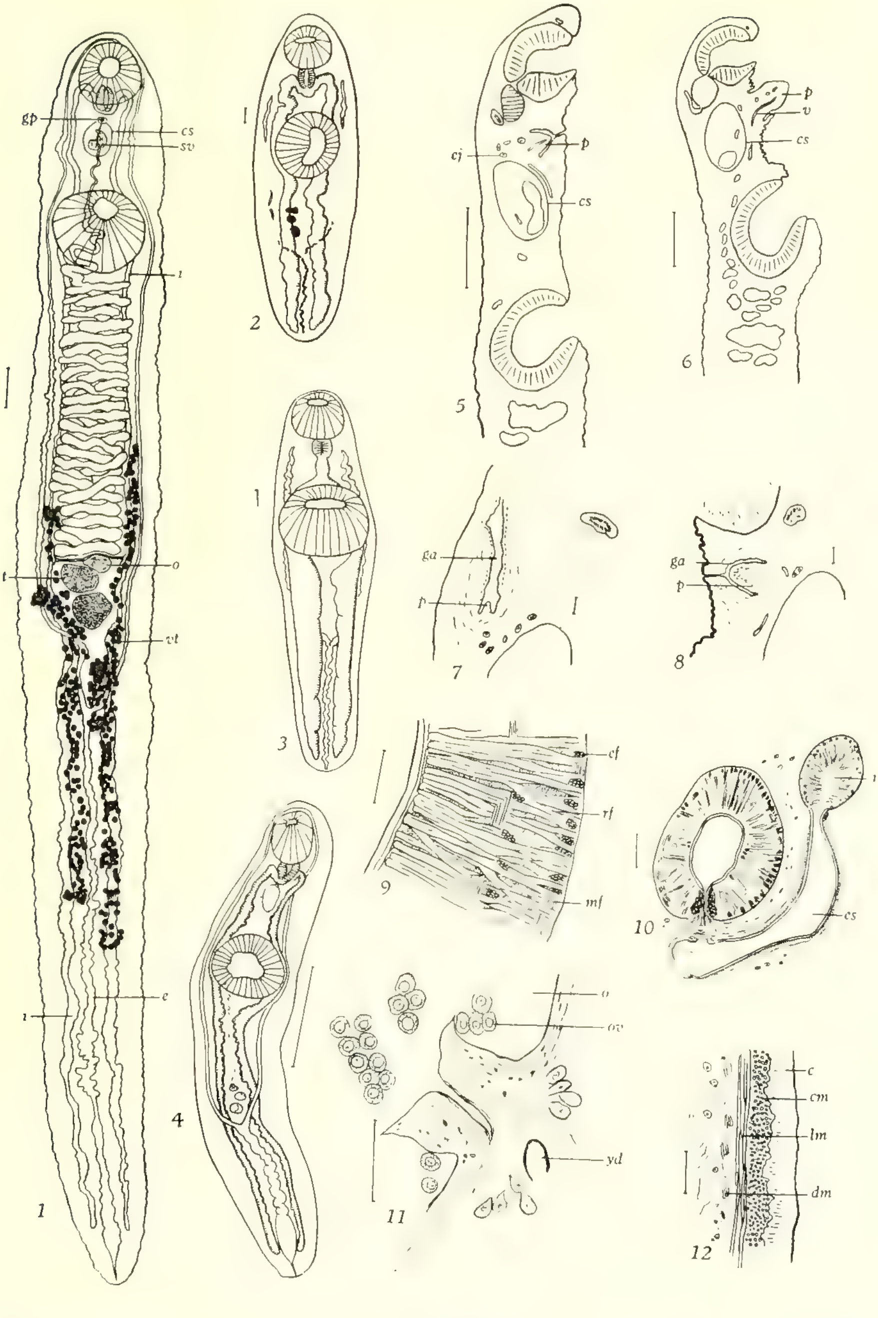
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PLATE II

EXPLANATION OF PLATE II

Figs. 13–18.	Outline drawings of gonads in *O. cestoides* to show changes in relative position of ovary.
Figs. 19–20.	Cross-sections of *Azygia sebago* to show inner parenchyma muscles.
Figs. 21–22.	Same of *A. acuminata.*
Fig. 23.	Same of *Otodistomum cestoides.*
Fig. 24.	Ootype region of *O. cestoides* to show relations of ducts. Semi-diagrammatic.
Fig. 25.	Cross-section through vas deferens of *O. cestoides.* Scale = 0.05 mm.
Fig. 26.	Sections through early eggs of *O. cestoides* before shell has assumed regular form.
Fig. 27.	Frontal section through uterus region of *Azygia angusticauda,* showing inner parenchyma muscles.
Fig. 28.	Sagittal section through genital atrium region of *O. cestoides* showing genital papilla retracted.
Fig. 29.	Same of *O. veliporum* showing genital papilla protruded.
Fig. 30.	Ventral view of anterior body region of *Azygia longa* showing position of genital pore. Scale = 1 mm.

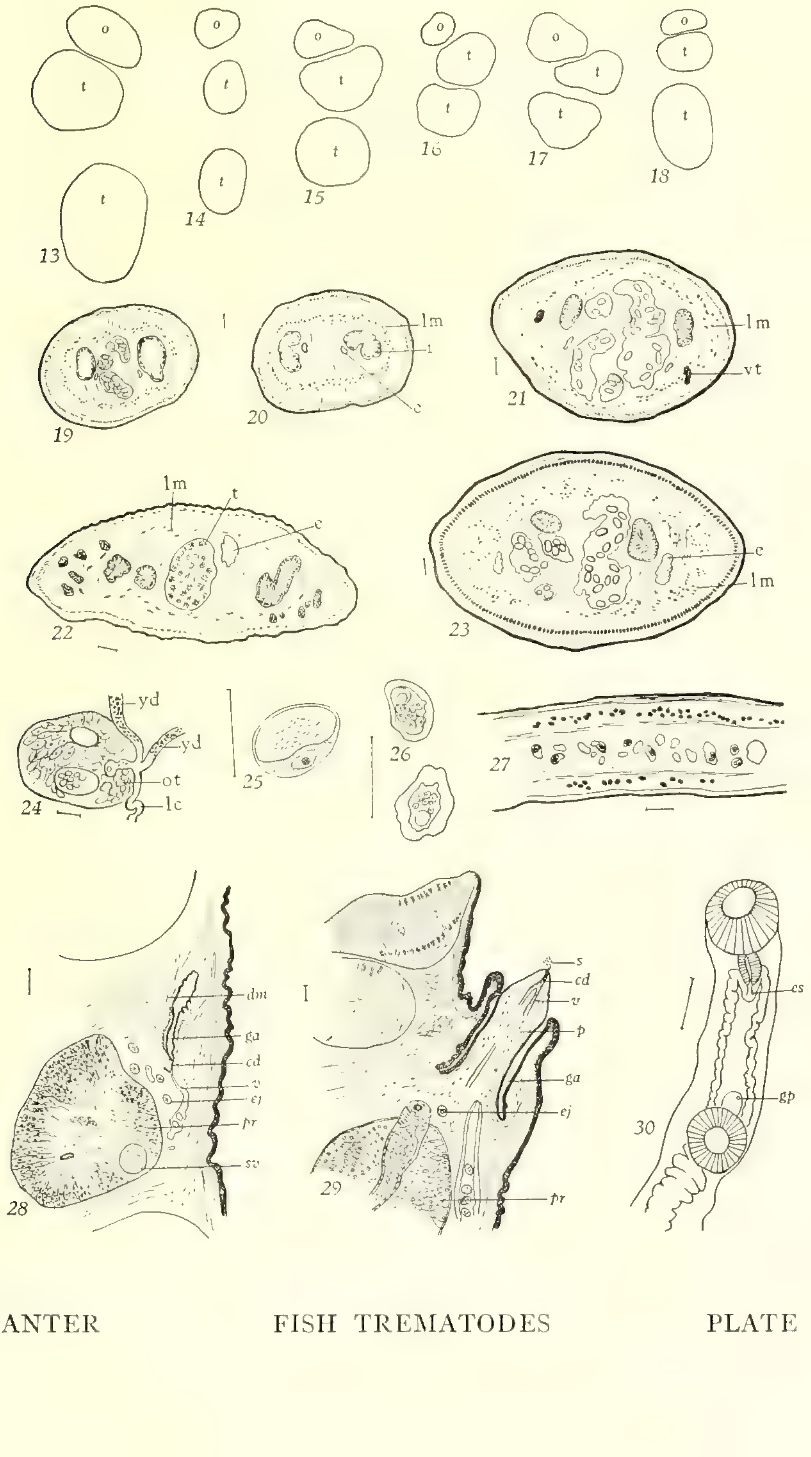
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PLATE III

EXPLANATION OF PLATE III

Fig. 31.	Mature egg of *Otodistomum cestoides*. Drawn from live egg. Scale=0.05 mm.
Fig. 32.	Same, showing three lobes in internal organ. Scale=0.05 mm.
Fig. 33.	Miracidium and empty egg shell of O. *cestoides*. Drawn from toto-mount. Length of larva 91u.
Fig. 34.	Recently dead miracidium of O. *cestoides* showing bristle plates detached. Scale=0.05 mm.
Fig. 35.	Cross-section through mature egg of O. *veliporum* showing the five bristle plates. Diameter of egg 50u.
Fig. 36.	Longitudinal section through mature egg of O. *cestoides*, showing paired glands.
Fig. 37.	Cross-section of same.
Fig. 38.	Longitudinal section through mature egg of O. *veliporum*.
Fig. 39.	Recently hatched miracidium of O. *cestoides*. Drawn from live specimen. Scale=0.05 mm.
Figs. 40–41.	Cross-sections through mature eggs of O. *veliporum*. Diameter of eggs about 60u.
Figs. 42–43.	Recently dead miracidia of O. *cestoides*, showing bristle plates. Scale=0.05 mm.
Fig. 44.	Longitudinal section of mature egg of *Azygia acuminata* showing four nuclei in internal organ. Length of egg 60u.
Fig. 45.	*Lepidapedon rachion*. Ventral view.
Fig. 46.	Sagittal section through region of ventral sucker of *L. rachion*.
Fig. 47.	Same of *L. elongatum*.
Fig. 48.	*Lepidapedon elongatum*. Ventral view.

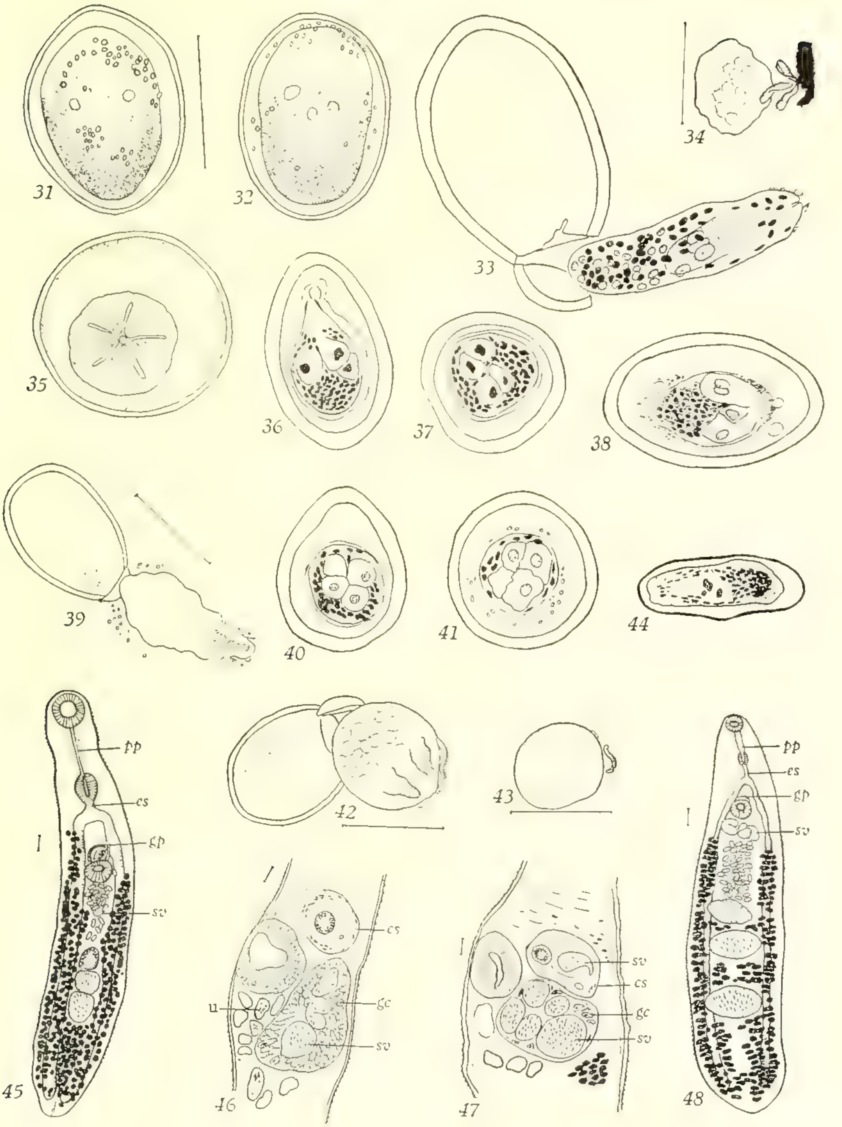
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PLATE IV

EXPLANATION OF PLATE IV

Fig. 49. *Podocotyle atomon.* Ventral view.
Fig. 50. *Podocotyle olssoni.* Ventral view.
Fig. 51. *Stephanochasmus baccatus.* Ventral view.
Fig. 52. Sections through eggs of *S. baccatus.*
Fig. 53. *Brachyphallus crenatus.* Ventral view.
Fig. 54. *Homalometron pallidum.* Ventral view of young specimen.
Fig. 55. *H. pallidum.* Sagittal section through region of seminal vesicle.
Fig. 56. *H. pallidum.* Ventral view of adult.
Fig. 57. *Derogenes varicus.* Ventral view.
Fig. 58. *Steganoderma formosum.* Ventral view.
Fig. 59. *S. formosum.* Cross-section through body just posterior to ovary.
Fig. 60. *S. formosum.* Sagittal section through posterior body region.
Fig. 61. *Lecithaster gibbosus.* Ventral view.

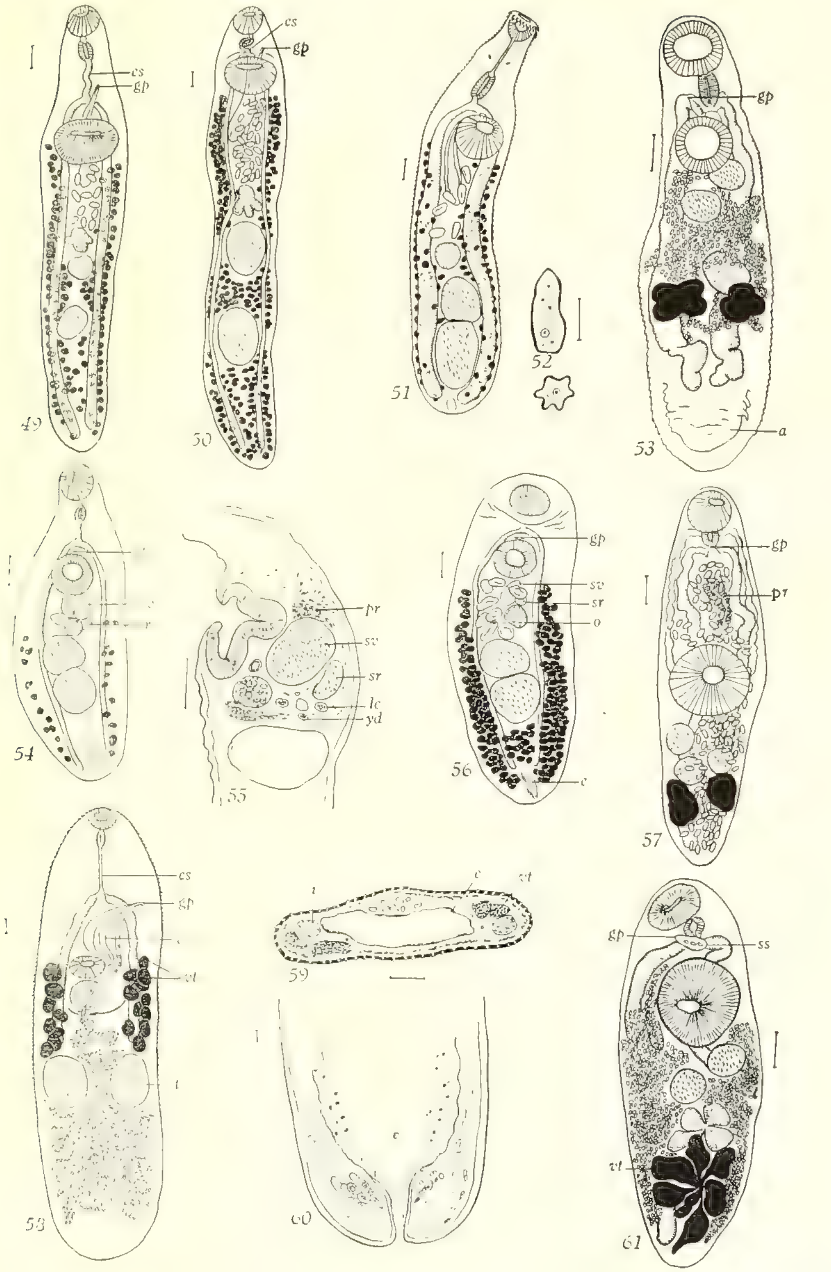
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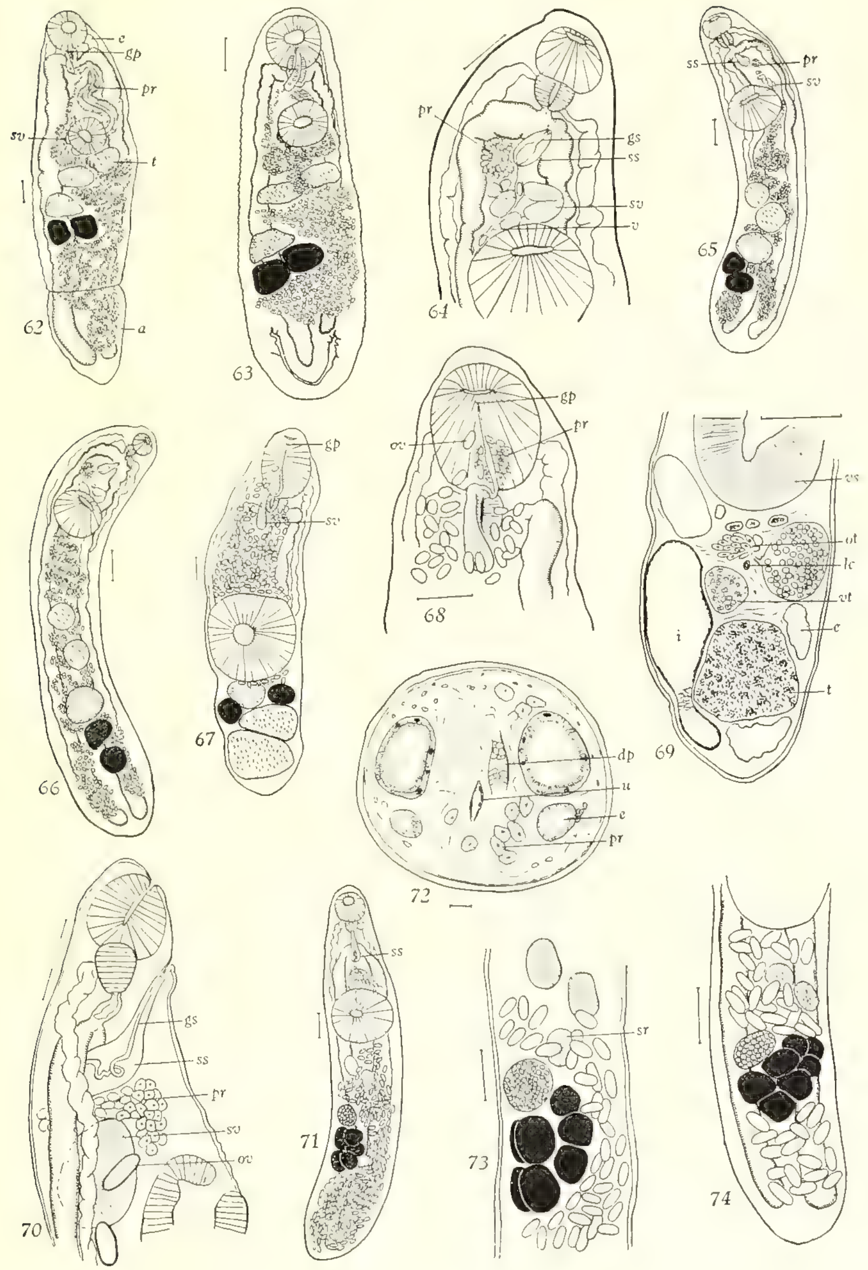
PLATE V

EXPLANATION OF PLATE V

Fig. 62. Ventral view of *Hemiurus levinseni* with tail appendage extended.
Fig. 63. Same, with tail appendage retracted.
Fig. 64. Ventral view of anterior body region of *Genolinea laticauda*.
Fig. 65. Ventral view of entire body of *G. laticauda*.
Fig. 66. Same view of another specimen.
Fig. 67. Ventral view of *Gonocerca phycidis*.
Fig. 68. Ventral view of anterior body region of same.
Fig. 69. Sagittal section through posterior body region of *G. phycidis*.
Fig. 70. Lateral view of anterior body region of *Aponurus sphaerolecithus*.
Fig. 71. Ventral view of entire body of *A. sphaerolecithus*.
Fig. 72. Cross-section through body of *A. sphaerolecithus* just posterior to sinus sac.
Fig. 73. Ventro-lateral view of body of *A. sphaerolecithus* in region of gonads.
Fig. 74. Ventral view of same.



MANTER FISH TREMATODES PLATE V

PLATE VI

EXPLANATION OF PLATE VI

Fig. 75. Sagittal section through anterior body region of *Hirudinella fusca*. Scale = 1 mm.
Fig. 76. Free-hand drawing of *H. fusca*, lateral view.
Fig. 77. Same, ventral view.
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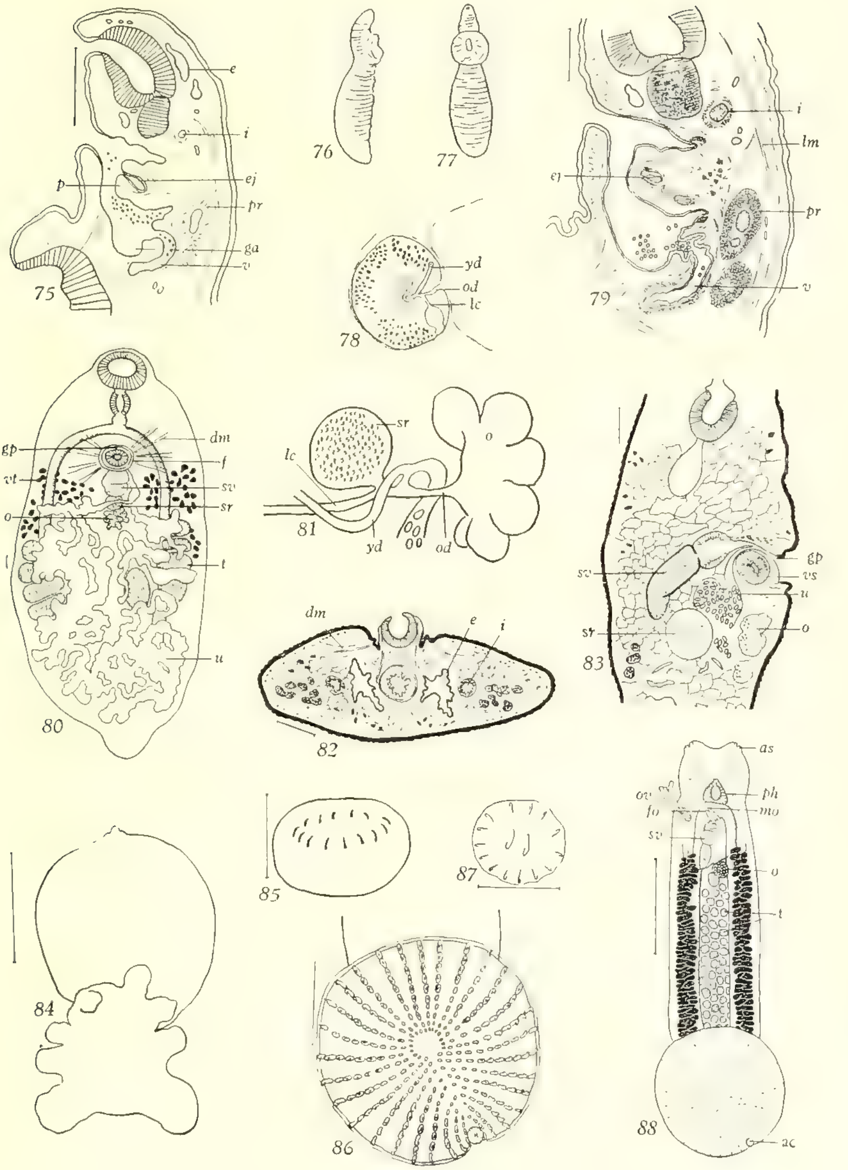
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